The Beagle

Records of the Museums and Art Galleries of the Northern Territory

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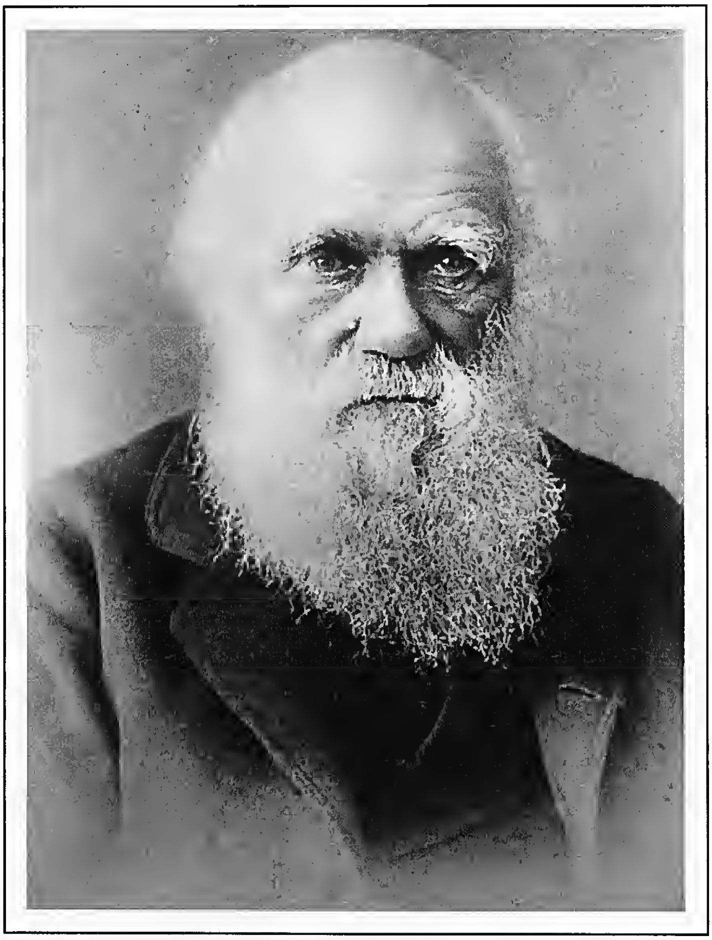

The Beagle, Records of the Museums and Art Galleries of the Northern Territory

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Australian Aboriginal, Southeast Asian and Oceanic art, material culture and archaeology;

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Front cover: In proposing his theory of evolution, Charles Darwin (1809–1882) caused a major shift in the way humans view the world. T year 2009 marks the 200th anniversary of Darwin's birth and the 150th anniversary of publication of his most influential work *On the Orig of Species ...* . His theory continues to spark debate (see pages 1–5). This photograph, taken by Elliott and Fry, is one of the last to be taken Charles Darwin. Photograph reproduced, with permission, from: Berra, T. 2009. *Charles Darwin: the concise story of an extraordinary ma* John Hopkins University Press: Baltimore.

RECORDS OF THE MUSEUMS AND ART GALLERIES
OF THE NORTHERN TERRITORY

Volume 25, December 2009

CONTENTS

Short communications

Charles Darwin: Shaping our Science, Society and Future

ABSTRACTS OF PRESENTATIONS

Since 2009 marks the 200th anniversary of the birth of Charles Darwin and the 150th anniversary of his most seminal work on evolutionary biology *On the Origin of Species* ... , the Northern Territory Government and Charles Darwin University sponsored a free public symposium held in the city of Darwin between 22 and 24 September to honour the life and achievements of this extraordinary man. His legacy has extended beyond biology and into the humanities and social sciences. This symposium presented opportunities to appreciate and debate Darwin's findings and his legacy. The symposium was organised under the Northern Territory Government and Charles Darwin University Partnership Agreement and arranged by a Steering Committee headed by Dr Richard Willan and Professor Robert Wasson representing the Government and the University, respectively.

Following a Welcome Reception at Parliament House hosted by the Chief Minister, The Honourable Paul Henderson MLA, delegates moved to the Darwin Convention Centre to hear a presentation on the life of Charles Darwin. The Symposium itself was divided into three themes across the next two days. National and international speakers reflected on the impact of Charles Darwin on their research in biology, medicine and history. The first theme was entitled 'Brave new world: what is Darwin's legacy in the era of modern medicine, biotechnology and technology-based societies?' The second theme was entitled 'Understanding the controversy between Darwinian science and religion'. The third theme was entitled 'Social Darwinism and indigenous nations: the origin of socio-political policy'. The titles of the presentations by the keynote speakers and their abstracts are as follows.

Charles Darwin: the concise history of an extraordinary man

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Charles Darwin is often considered the most influential scientist who ever lived because the theory of evolution is one of the most powerful ideas in science and may well be the greatest idea ever had by the human mind. 2009 is the 200th anniversary of Darwin's birth and the 150th anniversary of the publication of *On the Origin of Species* ... . His message of descent with modification through natural selection presented in 1859 in *The Origin* precipitated a paradigm shift – the replacement of one world view by another. Darwin changed the way humans view their place in nature. He showed that humans were not above nature, but part of it. He supplied an explanation for the great diversity of life and showed that all life, including human, is related by descent from a common ancestor. No other biologist has had an impact of this magnitude. In the words of the eminent geneticist Theodosius Dobzhansky: "Nothing in biology makes sense except in the light of evolution". The paradigm shift from creation to evolution has allowed a staggering array of advances in knowledge.

Darwin was born into a wealthy English family on 12 February 1809. He was educated at Edinburgh and Cambridge Universities and graduated 10th in his class of 178 at Cambridge in 1831. He was offered the unpaid position as naturalist-companion to Captain FitzRoy on the second voyage of H.M.S. *Beagle* from 1831-1836 on a surveying mission around South America. He considered this experience the first real education of his mind. The geology and biodiversity he experienced in rainforests, the pampas, the Andes, the Galapagos Islands, and on coral reefs influenced his thinking and the history of science. Darwin sent back 1529 species bottled in alcohol and 3907 dried specimens.

Darwin (1837) drew the first evolutionary tree to show the relatedness of all animal life. He explained how coral reefs form (1842) and contributed to geological observations on earth movements (1844) and the deformation theory of metamorphic rock (1846). He described all known barnacle species, fossil and living (1851–1854). Darwin explained how orchids are fertilised by insects (1862) and how plants climb (1865). He introduced the "control" in "controlled experiment" and he catalogued the bewildering variation in domestic plants and animals (1868). He explained human origins and sexual selection in ways never before articulated (1870–1871), and discussed human and animal emotions in similar terms (1872). The latter work was one of the first books to use photographs to illustrate a point. Darwin showed how insectivorous plants growing on impoverished soils utilise nitrogen-rich insects (1875), and he demonstrated that the offspring of cross-fertilised plants were more numerous and vigorous than self-fertilised ones (1876, 1877). His observations of climbing plants laid the foundation for the field of plant growth hormones (1880), and his work on earthworms (1881) is a classic study in ecology. Any one of these achievements could constitute a life's work for most scientists.

Evolutionary biology – the tree of life as a framework for comparative biology

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Evolutionary biology has undergone a renaissance of phylogenetic thinking and associated methods. While the phylogenetic concept has been around since Charles Darwin, only recently has the field of phylogenetics developed into a rigorous research endeavour. In this talk, I develop the idea of articulating evolutionary histories through the estimation of phylogeny, motivate the study of the Tree of Life, and provide examples of how this knowledge of evolutionary relationships provides a powerful tool to study a wide variety of questions in biology. I provide examples of the application of phylogenetic questions to organismal biology (Crustacea), medicine (infectious diseases including HIV) and conservation biology.

Co-evolution of infection and immunity

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Infection shows us evolution at work in our day-to-day world. The overall pace of genetic adaption for slowly-reproducing, multi-cellular, multi-organ systems like us is glacial when compared with the rate of change possible for the plethora of unicellular (bacteria, protozoa) or sub-cellular (viruses) organisms that seek to survive and multiply on our body surfaces (skin, mucosa) or within our tissues. As a consequence, vertebrates have evolved a very complex, broad-spectrum immune defence system to combat this process of parasitism. Conceptually, immunity is comprised of two distinct, but interactive components. Innate immunity provides a set of 'first response' mechanisms, some of which (like phagocytosis) go back to the very beginnings of biology. Elements of the slower-developing, but more targeted adaptive immune response are first seen in the lampreys and the jawed fish from 350–450 million years ago. Though birds and mammals share the basic characteristics of adaptive immunity, like specific 'killer' T cell and antibody-mediated effector function and memory, there has been considerable divergence through phylogenetic time in the way that the various elements are organized. When it comes to RNA viruses, we can see the interface between the selective pressures imposed by immunity and rapid molecular evolution operating at first hand, either on a population basis (influenza) or within the infected individual (HIV). Other one-host DNA viruses like the Herpesviruses and Poxviruses provide us with examples of long-term convergence as individual members of these virus groups have evolved much the same mechanisms to temper the consequences of immune control in the various species that they infect. In general, the fact that we can suffer autoimmune diseases makes it clear that immunity is an evolved rather than a designed system, with all the inherent compromises that are inevitable as species build on pre-existing mechanisms to adapt through time.

Drilling for Darwin: Rescuing the science of evolution from beneath layers of controversy

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"My Dear Darwin … I finished your book yesterday." With these words Thomas Huxley began his November 1859 letter to Charles Darwin that would presage a series of reactions to *On the Origin of Species* … . Darwin's bold model for the diversity of life that we see on Earth was indeed groundbreaking science. However, reactions to this new view were immediate and varied. Huxley ultimately saw this as an argument against the Church of England and the entrenched position of the clerics. Herbert Spencer, who coined the phrase "survival of the fittest", applied the evolutionary model to social, political, and economic systems. Darwin's cousin, Francis Galton, argued for steps to control the breeding of the human population in order to force the selection of certain traits, establishing the field of eugenics.

On the other side of the discussion, religious commentators were also reacting. Those who held to a literalist interpretation of Genesis were quick to argue against the implications of Darwin's proposal. Others, who were more in the mould of St. Augustine in their approach to scripture, could accept the scientific implications but were less convinced of the social and theological interpretations. In any case, it was clear that the science of biological evolution was quickly being buried beneath strata of controversial and decidedly non-scientific interpretative schemes.

This situation has continued until the present. We witness what the press calls the "evolution wars" being waged between the new militant atheists and the creationists and intelligent design advocates, each flying banners emblazoned with Darwinian, or anti-Darwinian slogans. And yet the science of evolution, especially when coupled with Mendel's understanding of inheritance, has become the central paradigm of biology, leading us to an expanded understanding of how the living world functions.

All of these positions are scientifically and philosophically flawed. Creationism and intelligent design are not scientific and also not theologically sound. The neo-atheist position may have philosophical positions, but these conclusions are not directly related to or provable by the science of evolution.

I propose a different approach. Theistic evolution is the broad and peaceful middle ground between these factions. In this view, the science of evolution is championed as the most reasonable explanation for the observed data, and the model that has been most fruitful in opening new avenues of investigation. However, the theological, philosophical, and social arguments are pried away from the scientific framework. For a theistic evolutionist, a belief in God is not in opposition to the science of evolution. While an atheist may disagree with this, the science of evolution does not justify that disagreement.

Darwin and the ascent of emotionally modern man: how humans became such other-regarding apes

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As proposed by Charles Darwin, humans are remarkably similar to other apes. Like their larger brained, bipedal 'cousins', Great Apes also use tools and exhibit a rudimentary understanding of causality and Theory of Mind. However, other apes fall short of humans in intention-reading and co-operation. In this lecture I explain why I am convinced that the psychological and emotional underpinnings for apes to care so much about what others intend and feel emerged as a by product of shared parental and alloparental care and provisioning of young, what sociobiologists refer to as 'co-operative breeding'. According to widely accepted chronology, large-brained, anatomically modern humans evolved around 150 000 years ago, and behaviourally modern humans, capable of symbolic thought and language, more recently still, between 50 000–80 000 years ago. But (I argue) emotionally modern humans, newly interested in the mental and subjective states of others and characterised by prosocial impulses to give and share, emerged far earlier along with what, for an ape, was a peculiar mode of rearing young.

Indigenous epistemologies and social Darwinism

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During Charles Darwin's voyage in the South Pacific in the 1800s, the foundations of modern scientific research and its ontological and epistemological pillars were being set in history. The inclusion of Pacific Indigenous peoples within such history was always as an object of study and never the producer or the consumer of research. Modern science today and its investigative methods are not detached from the social and historical circumstances of its origin. This paper will argue that from across Darwin's 'imagined' South Pacific, Indigenous researchers are forging a new intellectual agenda which I call Contemporary Critical Indigenous Scholarship. This agenda seeks new and robust ways to conduct research while revealing insights on the role the Indigenous intellectual.

Darwinism and the Victorian soul: the reception of Darwin's theory of human evolution in the 19th century and beyond

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In an 1871 cartoon in the British magazine *Punch*, an earnest young husband reads to his wife and infant child from Charles Darwin's just-published book *Descent of Man*. "So you see, Mary, baby is descended from a hairy quadruped, with pointed ears and a tail," he explains. "We all are." His wife counters: "Speak for yourself, Jack. I'm not descended from anything of the kind, I beg to say; and baby takes after me."

This was the general attitude toward the question of human evolution in much of English-speaking world at the time *Descent of Man* arrived, a question cast into the spotlight by British naturalist Charles Darwin. Although the general concept of organic evolution was quickly and widely accepted by British and American scientists and much of the educated public, the specific case of humans – or at least distinctly human characteristics – proved more problematic. From the time his *On the Origin of Species* ... was published in 1859, scientists and others on both sides of the Atlantic had hotly debated the proposition that humans evolved from animals even if they accepted evolutionism generally. Review the editorial cartoons, read the scientific commentary, and the basic sentiment toward the idea is almost always the same: Most people simply refused to believe their highly developed minds, morals or emotions evolved from those of beasts.

In some ways, little has changed in the past century. Many otherwise committed evolutionists draw the line on materialism when it comes to the ascent of man. Oxford ornithologist David Lack, whose 1947 study of Darwin's finches gave wing to the modern neo-Darwinian synthesis, believed: "Science has not accounted for morality, truth, beauty, individual responsibility or self-awareness, and many people hold that, from its nature, it can never do so." The American geneticist Francis Collins, who directed the Human Genome Project and now heads the National Institutes of Health, wrote: "Science will certainly not shed any light on what it means to love someone, what it means to have a spiritual dimension to our existence, nor will it tell us much about the character of God." His words continue a debate that began in the Victorian Era.

RNA as the engine of complexity: a new view of human evolution and genomic planning

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It appears that the genetic programming of humans and other complex organisms may have been misunderstood for the past 50 years, because of the assumption – largely true for prokaryotes, but not for multicellular eukaryotes – that most genetic information is transacted by proteins. The human genome comprises three billion base pairs of DNA sequence information. It programs the development of a precisely sculptured individual of about 100 trillion cells with hundreds of different muscles, bones and organs, as well as the brain. It contains about 20 000 conventional protein-coding genes, surprisingly about the same number and in large part with similar functions as those in tiny worms that have only 1000 cells. On the other hand, the extent of non-protein-coding DNA does increase with increasing complexity, reaching 98.8% in humans, suggesting that much of the information required to program human development may reside in these sequences. This is supported by the observation that regulatory information scales quadratically with function, indicating that as complexity increases a greater proportion of the genome is devoted to regulation and that prokaryotes were limited in their complexity by a protein-based system, a problem the eukaryotes solved as a prerequisite to the appearance of developmentally complex species in the Cambrian.

Consistent with this proposition, recent studies have shown that the majority of the mammalian genome is transcribed, mainly into non-protein-coding RNAs, and that there are tens of thousands of long and short RNAs in mammals that show specific expression patterns and subcellular locations, especially in the brain. There is increasing evidence that these RNAs control gene expression at many levels, and comprise a massive hidden regulatory network that directs the precise patterns of gene expression during growth and development. Indeed, RNA-directed regulatory circuits underpin most, if not all, complex genetic and epigenetic phenomena in eukaryotes. Moreover, the editing of RNA (which has expanded in the vertebrates and especially in the primates) appears to be the means by which environmental signals modify epigenetic

information, especially in the brain, thereby comprising the molecular basis of learning and the evolution of cognition. Thus, rather than simply being a passive intermediate between DNA and protein, RNA may represent the computational engine of the cell, becoming become progressively more sophisticated in more complex organisms. Thus, what was dismissed as junk because it was not understood may hold the key to understanding human evolution, development and intelligence, as well as our physical and psychological idiosyncrasies and susceptibilities to common diseases. Finally, the observation that some RNA-directed epigenetic changes can be inherited raises the intriguing question: has evolution learnt how to learn?

The then and now of Social Darwinism for Indigenous Australia: imagining a different future

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The bi-centenary of Charles Darwin's birth could also mark the end story of Social Darwinism in Australia. But an alternative narrative of country and race requires a paradigm shift in which the evolutionary gaze is swung 180 degrees from the Indigene to the non-Indigene: a re-imagining of non-Indigenous self-concept and belongingness. This paper develops this idea by juxtaposing eras of Darwinian influenced terrain: the 1830s and 1840s and the 1990s and 2000s with a different vision for the era 2010 onwards. In February 1836, when Darwin visited what was known to the Europeans as Van Diemen's Land, he had no or little contact with Aboriginal people. By then the last traditional people were imprisoned and dying at Wybalenna. If we fast forward to 2009 and imagine Darwin revisiting, again his Aboriginal contact would likely be sparse. Except in commodified objects such as dot paintings, or as anthropological curiosity, the Indigenous is absent from the nation's view of itself and Indigenous peoples remain locked in what I refer to as the domain of Aboriginality. Darwin's work rationalised the Tasmanian destruction post event via the concepts of evolutionary inevitabilities and Social Darwinism and Darwin himself contributed by requesting Tasmanian skulls. In contemporary times the iterations and societal adaptations of these concepts still echo into Indigenous lives. The socio-cultural hierarchy replaced the Chain of Being, but the imprint of the latter is embedded in the shape and interpretation of the former. How can the post-2010 era be different? The paradigm shift I propose reverses the discourses of evolutionary inevitabilities with the pivotal re-imagining the narrative of non-Indigenous evolvement of interaction and relating to country, perceptions of Australia's identity and conceptions of fit within the land and its heritage. Indigenous understandings and peoples are inevitably central to these imaginings.

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The role of textiles in the royal funeral of Ain Le'u, Biboki, West Timor, Indonesia

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ABSTRACT

This paper explores the role and cultural significance attributed to textiles in the mortuary practices of the Atoin Meto people of West Timor, Indonesia, and the use of textiles as markers of extraordinary events. It also considers forms of foreign influence on attire and cultural practices. The case study of the royal funeral of Ain Le'u, the wife of the customary ruler of Biboki, in Kaubele, North Biboki, in 2006 provided the lens through which to observe and document the employment of various types of textiles, including the handwoven warp ikat textiles that feature indigenous motifs, in Biboki mortuary practices.

Keywords: Atoin Meto, textiles, Biboki, West Timor, mortuary practices.

LANGUAGE KEY

Bahasa Indonesia = *(I)*	Latin = *(L)*
Bai Keno / Uab Meto language = *(BK)*	Tetun = *(T)*

INTRODUCTION

Ain Le'u, the much loved wife of the Kaiser of Biboki, died on 12 March 2006.[1] I'd had the pleasure of meeting Ain Le'u in 2004 in Kefamenanu and she was a most gracious and urbane woman. 'Next time you're in Timor, please come and visit us in Kaubele', were her parting words to me. Little did I know that it would be her royal funeral on 17 and 18 March 2006 that finally took me to Kaubele village in north Biboki, North Central Timor (TTU), West Timor, where she had resided with her husband the Kaiser of Biboki, until the time of her death.

As a participant at Ain Le'u's funeral I was given permission to document her funeral and witness the proceedings that are recorded in this paper. I also had the opportunity to discuss aspects of the ceremonies I witnessed with prominent members of the Biboki community during and upon completion of the funeral.

Kaubele has been the home of the Kaiser of Biboki[2] over several centuries, Biboki being one of ten princely states into which West Timor was divided in the late colonial period.[3] Kaubele's northern, coastal location historically enabled the Kaiser to oversee trading arrangements between the largely inland Biboki Kingdom and foreign traders from Java, South Sulawesi and China who frequented Timor's coast from as early as the 12th century (Gunn 1999: 52–53). European traders frequented the area from the 16th century onwards. Kaubele's location near the coastal ports of Mena and Atapupu would have facilitated the Biboki Kingdom's access to trade goods and luxury items in return for local produce of sandalwood, beeswax and human slaves.

However, the cultural and ceremonial centre of Biboki Kingdom is located at Tamkesi, approximately 50 kilometres inland from Kaubele (Fig. 1). Tamkesi, often referred to as the 'sacred heart of Biboki', is built on a rocky outcrop high on a mountain with expansive views over the Biboki lands[4]. It consists of two hilltops linked by a ridge, representative of cosmic dualism which permeates the Atoin Meto world view[5].Tamkesi continues to be the ritual centre of the Biboki realm, where cultural knowledge is upheld and preserved. The Kingdom's sacred relics, *le'u (BK),* have customarily been stored at Tamkesi due to its inland location, which provided greater protection from intruders[6].

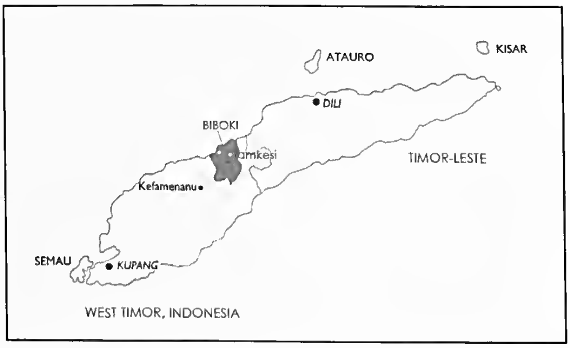

Fig. 1. Map of Timor indicating Biboki, Kaubele and Tamkesi.

It was at the foot of Tamkesi, in the village Tautpah that Ain Le'u was born in 1920 to parents of Atoin Meto and Chinese ancestry. In this region Chinese traders successfully intermarried with aristocratic families, thus strengthening trade relationships, routes and economic power. Ain Le'u, whose given name was Lidwina Us Boko, married the current Kaiser of Biboki, Tnesi Iba Us Boko, the customary leader of Biboki culture[7]. Ain Le'u was a mother of four children, a grandmother to eighteen grandchildren and a great-grandmother to eleven great-grand children. The widespread respect and affection inspired by this Biboki queen was enshrined in her name, Ain Le'u, which translates to 'Sacred Mother'[8].

CLOTH IN LIFE CYCLE RITUALS

Observing and participating in Ain Le'u's funeral provided insights into contemporary Atoin Meto mortuary and cultural practices. In particular, this occasion provided a lens through which to view the specific role and function that textiles perform in this major life cycle event[9]. Cloth is universally present at life cycle events in Timor and eastern Indonesia, where textiles have been widely regarded and documented as important elements of life cycle rituals, used as attire, banners, mats, hangings and shrouds (Gittinger 1979; Maxwell 2003). In addition to serving functional purposes, textiles also operate as markers that indicate something extraordinary is happening. As forms of exchange used by Timorese people and cultures they:

> … signal and materialise the establishment, renewal and termination of relationships. Messages of ethnicity, sense of place, gender, age, social rank political legitimacy and community longevity are contained within textiles. They convey ancestral tradition cross generationally, using a language of form and aesthetic that is deeply imbedded in local cultural consciousness. They can also be important vehicles of magical power, cocooning and protecting both people and objects from physical and metaphysical ills (Leibrick 1994: 9).

THE FUNERAL PREPARATIONS

Upon news of Ain Le'u's death and the announcement of the location of her funeral, people began travelling to Kaubele village. Ain Le'u's funeral was the first royal burial to occur outside the sacred Biboki centre of Tamkesi. This decision marked a departure from local cultural tradition. This choice of venue, determined by Ain Le'u's children, highlighted current shifts and tensions within Atoin Meto society between tradition, customary practices and modernity. The family made a public commitment at the funeral to conduct a secondary burial in the future at which time Ain Le'u's remains will be relocated to Tamkesi[10].

Approximately 2500 people from across the Biboki Kingdom, both commoners, *amat (BK)*, and aristocrats, *usif (BK)*, walked for over two days and nights to Kaubele village to attend Ain Le'u's funeral, which was held on Friday 17 and Saturday 18 March 2006 at the Kaisers's family house. Atoin Meto people from all the Biboki clans, along with representatives from the neighbouring Atoin Meto regions of Insana and Miamafo, attended her funeral. Delegations of Tetun people from Belu joined Savunese, Rotinese mourners, all of whom converged in Kaubele to pay homage and farewell Ain Le'u to the afterlife.

The official commencement of mourning was marked by the lighting of a fire outside the front of the Kaiser's house. This fire known *Ain No'no (BK),* continued to burn from the time of death until the interment of the corpse, which marks the formal completion of the funeral ceremony. The slow burning *kusambi* wood, *Schleichera oleosa (L)*, is used for the *Ain No'no* fire. This wood features in Atoin Meto ceremonies of birth and death[11]. During and following birth it is burnt inside the house. At times of death the *kusambi* wood is burnt outside, locating this life cycle ritual within the Atoin Meto world view of binary opposition, in this instance expressed through the dichotomy of the inner and outer realms.

The *Ain No'no* fire's purpose was to 'heat' the ceremony and to guard Ain Le'u on her journey to the afterlife. This is in keeping with the extraordinary, dangerous heated state induced by Ain Le'u's death. Only once the funeral is completed can the 'cool' state, denoting safety and calm, return. Hence, the forming and lighting of the fire was a protective device, which was the specific responsibility of three Biboki clan groups, Naek Le'u, Subun and Tas Au[12]. Senior clan representatives were duty bound to guard the fire, day and night, until Ain Le'u's body was finally interred.

With the *Ain No'no* fire lit three days before the funeral, people began to gather at the Kaiser's family house. Upon arrival, mourners were greeted by the Kaiser who was inside the mourning room or near the *Ai No'no* fire. The Kaiser wore his headscarf, *piln (BK)*, slanted to the right side, symbolic of his wife's death and his state of mourning in the sphere of death. Following the conclusion of the ceremony, the peak of his *piln* would be worn in a central position signifying his return to the sphere of life (Meta pers. comm. Kaubele, 17 March 2006). Such practices are consistent with mortuary practices described by Middlekoop (1963: 26).

The procession of mourners was invited to enter the front living room where Ain Le'u lay in state. As each new guest or group of guests[13] entered the room a metal gong, *sene (BK)*, was struck by a male chief mourner. Each arrival was announced by seven strikes of the gong[14]. In keeping with Atoin Meto tradition, many men and women entered the mourning room by crawling in on their knees and wailing, *litu (BK).* While paying homage to Ain Le'u many women wore their hair loose as a sign of grief[15]. This practice is in direct contrast to the social expectation that respectable Atoin Meto women must tie up their hair in public[16].

Fig. 2. A canopy of a man's single warp ikat cloth wrap protects Ain Le'u's coffin. Other woven textiles gifted by mourners are hung delineating the mortuary space.

All photographs by Joanna Barrkman.

Fig. 3. Handwoven textiles gifted by mourners are hung delineating the mortuary space.

Fig. 4. Women enter the mortuary space bearing handwoven cloths in baskets as offerings to Ain Le'u's family.

Ain Le'u's body lay in state inside the front room of the house, within an open wooden coffin[17]. The primary mortuary space was defined by the use of suspended white cotton curtains, which delineated the space around the coffin (Figs 2–4). However, at no time were these curtains drawn closed. Suspended above the coffin was a canopy, *neoba (BK)* (Fig. 2), consisting of a men's cloth wraps, *beti naek (BK)*. This cloth wrap, woven in the warp ikat technique, *futus (BK)*, featured a *beti klaut* motif. This canopy served to delineate the sacred mortuary space while also physically protecting the corpse from dust and dirt (Philipus Manek pers. comm. Kaubele, 18 March 2006). Beneath the canopy the open coffin was draped with a white tulle cloth shroud with embroidered edges (Fig. 5). This transparent cloth was referred to as *kain tele (BK)* and featured an embroidered Christian crucifix in the centre field, denoting Ain Le'u's adherence to the Christian faith.

Ain Le'u's corpse wore a hand woven tube skirt, *tais feto (BK)* (Fig. 6), which she had made prior to her death using commercially spun cotton and a combination of chemical and natural dyes[18]. It is likely that she made this tube skirt with the intention of wearing it as her burial attire as it is customary in Atoin Meto society for women of mature years to weave a special cloth intended for this purpose (Meta cited in Bennett 2005: 26).

The *mak'aif* motif is featured on the tube skirt worn by Ain Le'u. This motif depicts a series of hooks in a lozenge form (Fig. 6) and is ubiquitous in Biboki textiles. According to one interpretation, it represents the linked arms of dancers and is a metaphor for social harmony (Meta cited in Bennett 2005: 26). Ain Le'u had chosen to weave a *mak'aif* motif known as *Fut Mak'aif Hint* featuring seven hooks. According to local conceptions the wearer's social status is indicated by the number of *mak'aif* included in the motif. In this instance the use of seven *mak'aif* signified Ain Le'u's high social position. A relationship exists between the *mak'aif* motif woven into Ain Le'u's tube skirt and the *beti klaut* motif woven into the warp ikat canopy cloth. These two motifs form a pair of complementary opposites, likened to a bow and arrow[19] (Yovita Meta pers. comm. Kefamenanu 2005). The use of this complementary pair of motifs and

Fig. 5. Ain Le'u's corpse covered with a tulle cloth decorated with a Christian crucifix.

Fig. 6. Ain Le'u's corpse attired with a tubeskirt featuring motif *Mak'aif Huit*, a white lace *kebaya*, gloves and head dress. Gifts of cloths and toiletries had been placed into her coffin.

textiles supports the claim that clothing, in Southeast Asia is an important symbol of status for the dead, as well as the living, as a system of signals intended for supernatural beings (Maxwell 2003: 114).

In addition to these indigenous motifs and paired cloths, other foreign influences were evident in Ain Le'u's mortuary attire. Ain Le'u wore a pair of white gloves and a white lace blouse, *kebaya (I)*. The *kebaya* is a traditional form of Malay women's attire, commonly worn in Sumatra, Malacca and Java from the 19th century onwards. It is an adaptation of the *baju panjang* or long-sleeved blouse that is thought to have been introduced into the Malay archipelago by Arab traders, whose adherence to the Muslim faith prohibits women exposing their shoulders and upper arms. The *kebaya* became an accepted part of traditional Javanese attire and its influence extended to eastern Indonesia in the late 19th and early 20th century, where it has replaced the tradition of women wearing a tube skirt tied either beneath the armpits or waist, leaving the upper body exposed. The incorporation of the *kebaya* into eastern Indonesian cultures, such as the Atoin Meto, was advocated by Christian Dutch colonialists, who also embraced the *kebaya* as a form of attire. The *kebaya*, therefore became a symbol of status amongst Atoin Meto society, indicative of a cultured, modest woman of high status and Christian faith. Another consequence of Dutch influence evident in Ain Le'u's funeral attire was her wearing a pair of white gloves. The practice of wearing white gloves in Atoin Meto culture occurs at both weddings and funerals and is indicative of the formal nature of the occasion.

In addition to this ceremonial attire, Ain Le'u wore a white cotton headband known as a *tain pele (BK)*, adorned with numerous silver coins. *Tain pele* are only worn for death rites. This headdress exists in partnership with its counterpart Atoin Meto headdress, known as *pet no'o (BK)*, the traditional silver headdress worn during ceremonies by the living. A silver decorative hair comb, *kiln none (BK)*, also made from smelted foreign coins, rested above Ain Le'u's head. Dutch, Portuguese, Mexican and Indian silver alloy coins that had entered Timor during the Dutch and Portuguese colonial eras were sought by local silversmiths and forged into local body adornment (Rodgers 988: 31; Barrkman 2009: 35, 101–108). Ain Le'u also wore a necklace of Indian glass beads, *molo (BK)*, silver bracelets, *niti (BK)*[20] and a rosary. Personal belongings such as eye glasses, a hand mirror, a pair of shoes, a makeup purse, a travel blanket, toothbrush and paste were also placed within Ain Le'u's coffin, as these were considered by her immediate family as necessities for her imminent journey to the afterlife.

GIFT GIVING

Mourners made offerings of customary gifts to Ain Le'u's family including money, cloths (Fig. 3), rice, bracelets and animals (such as goats, pigs and cows). However, it was cloth that formed the primary exchange commodity to fulfil obligatory relationships between the mourners and the family of Kaiser and Ain Le'u. In some instances, the cloth offerings were chosen to be hung above the coffin. However, the majority of the gifted cloths were retained by the family to be counted and noted, so that in the future the same 'value' of gift can be reciprocated to the giver's family as occasion determines. Ain Le'u's family eventually divided the cloths amongst themselves, ensuring that each branch of the family had a suitable store of textiles to fulfil their future gift-giving obligations (Yovita Meta pers. comm. Kaubele, 18 March 2006).

It is common in West Timor that gifts are given to indicate the prestige and wealth of the deceased and the powerful connections of the extended family (Coury 2004: 48). The use of textiles in funeral arrangements emphasises the social order of the living and the dead. In such cases textiles, considered a 'female' form of gift, are usually presented by one set of relatives and different types of 'male' grave goods, such as livestock, are presented by another set of relatives (Maxwell 2003: 114).

From amongst the hundreds of cloths gifted to Ain Le'u and her family, specific tube skirts, *tais feto (BK),* and men's wraps, *beti naek (BK),* were chosen to be hung from the canopy surrounding her coffin (Figs 2 and 4). Other gifted textiles were selected by the family and placed inside Ain Le'u's coffin, to accompany her to the afterlife.[21] Cloths selected for this purpose denoted specific clan alliances and relationships. One example of an intricate tube skirt with a motif from the Insana Kingdom was rolled up and strategically placed in Ain Le'u's coffin (Fig. 6). This symbolised the relationship between the royal Us Boko clan of Biboki Kingdom and the royal Us Finit clan of Insana Kingdom.[22]

Another tube skirt selected for inclusion in Ain Le'u's coffin was a hand spun and naturally dyed tube skirt known as *tais ha ma buna (BK),* which featured the single warp ikat motif *mak'aif nim (BK)*[23]. It also featured three bands of motifs woven using the intricate discontinuous supplementary weft wrapping technique known as *buna.* This weaving technique is a significant marker of status on Atoin Meto women's textiles. Three or more bands of *buna* motifs are only permitted to be worn by aristocratic women, who traditionally were the master weavers, having access to the requisite materials and time to execute the production of such complex textile techniques.

The choice of this gifted tube skirt given to accompany Ain Le'u to the afterlife was determined by the strong allegiance that exists between the Nahas clan of Sainup village and the royal Us Boko clan[24]. This relationship eventuated due to military support provided by the Nahas clan to the Kaiser of Biboki that resulted in the Nahas clan being bestowed with land and a marriage alliance with the royal Us Boko clan. However, before this magnificently woven tube skirt, produced by Belendina Kela of Sainuip village, could be placed into the coffin, Ain Le'u's daughter was invited to cut into the edge of the *buna* decoration on the tube skirt. Using a small pair of scissors to perform this act, it ensured the cloth's imperfection, thus making it an accurate reflection of the mundane, imperfect world of the living – in contrast to the perfect, ideal world of the ancestors, to which Ain Le'u was destined[25].

Fig. 7. Martha Ane wearing a *peak metan*, symbolic of her state of mourning.

MOURNING ATTIRE AND CEREMONIAL PARAPHERNALIA

Public displays of grief were evident in the attire worn by the mourners. As the elders of the clans gathered on 17 March 2006 to sing mourning song cycles known as *Boin Nitu*[26] and to dance the *bonet boen nitu* and *naben* dances throughout the night preceding the funeral, hundreds of the mourners wore a small black swatch of cloth pinned to their garments (Fig. 7). These black cloth swatches are known as *paek metan (BK).* This practice of wearing a black swatch of cloth occurs in both West Timor and Timor-Leste, suggesting it is derived from Catholic and European influence. While its origins are likely to be found in Catholic practices, in Timor island both Protestants and Catholics

Fig. 8. Kaiser Us Boko with his children in mourning attire at Ain Le'u's funeral.

Fig. 9. Priests perform a Catholic Mass at Ain Le'u's funeral service with robes adorned with Javanese batik cloth.

Fig. 10. A woman is dressed in attire denoting Ain Le'u's royal status enabling her to adopt the role of Ain Le'u's living representative during the funeral ceremony.

alike wear *paek metan*. These public signs of mourning are worn for a minimum of forty days up to as long as ten years following the death of a family member. The Kaiser, as Ain Le'u's chief mourner, was expected to wear his *paek metan* for a minimum period of five years (Yovita Meta pers. comm. Kaubele, 18 March 2006). Upon the completion of the mourning period, the *paek metan* is either ceremonially released into a flowing river or else it is burnt[27].

As another sign of mourning, people wore plain 'everyday' clothes as opposed to their ceremonial *tais* or *beti naek*. Prohibitions during mourning, such as a taboo on wearing the colour red, with the exception of the chief mourners, were also respected. This is due to the association of red with celebration and power and as the traditional colour of rulers and the attire of *meo, (BK),* head-hunters. Ain Le'u's Chinese ancestry was evident through the attire worn by the primary mourners, her four children. They wore white shirts with their traditional Biboki attire during the formal funeral proceedings, upholding the Chinese custom of wearing white as a sign of purity and respect at funerals.

On the morning of 18 March the formal funeral proceedings began. Several pigs were slaughtered with the intention of guarding Ain Le'u's descendants against ill health and disaster. An indigenous mourning ceremony and a Catholic Requiem Mass officiated by three Atoin Meto priests occurred simultaneously. Several warp ikat textiles featuring Biboki motifs were chosen to form a backdrop to the pulpit where the priests delivered their sermon, providing another example of indigenous cloth being used to delineate sacred space. Beneath the pulpit, altar boys performed their incantations and burnt incense in front of both the priests and the ceremonial *Ai No'on* fire, which continued to burn. The priests' vestments included Javanese batik textiles (Fig. 9). Formerly considered as a foreign and 'outside' commodity, Javanese batik enjoyed prestige in Atoin Meto society over several centuries where its incorporation into local attire as men's head scarves, *pilu (BK),* or as women's sarongs denoted exclusivity, status and privilege. In the contemporary era, the use of commercially printed batik cloth is commonplace and readily accessible to the wider population.

In conjunction with the Mass, indigenous mortuary rites were performed. These rites were performed upon completion of the Mass, with no apparent disapproval from

Fig. 11. A senior man holds *katkiti*, a bundle of offerings of jewelry and money that were later carried in the funeral procession for Ain Le'u.

the officiating priests. Prior to the commencement of the Mass, a woman appeared in the front of the gathering and publicly became dressed as a *meo (BK),* warrior (Fig. 10). This was a symbolic representation of Ain Le'u on the earth plane. She wore a headdress, *tain pele (BK)*[28], made from a red cloth, and a set of seven sacred breast-discs, *neon (BK),* that earlier had been hung above Ain Le'u's coffin. These breast-discs were removed from the wall and placed around her neck, symbolic of her assuming a living form of Ain Le'u during the ceremony. She then proceeded to sit beside the *Ai No'on* fire, as a representation of Ain Le'u, during the Mass and other proceedings.

This phenomenon of women dressing in *meo* head-hunting attire traditionally occurs at life crisis rites[29]. The daughters of great head-hunters traditionally would wear *meo* attire and dance at their father's funeral (Gittinger: 1979: 179). Upon return to society following a period of confinement of forty days after child bearing, traditionally the woman emerged wearing the *meo* attire of her husband, indicating her warrior-like status achieved by surviving the life-threatening event of childbirth. This ceremony is known as 'touching the ground'. As a symbol of fertility, the mother was adorned with ritual head-hunters' regalia on the occasion of introducing her newborn child to the clan, ensuring continuance of the lineage. Women also wore head-hunters' attire for the *Ta Poen Olef* ceremony, which requests the skills for life for newborn children[30]. In the instance of Ain Le'u's funeral the physical 'presence' of Ain Le'u as a *meo* warrior affirmed the imminent and potentially dangerous journey awaiting Ain Le'u as she departed the mundane world and undertook to enter the world of her ancestors. She sat in the front of proceedings and oversaw the event. At her feet, a ritual known as *Tapan Mof Nes Nabala* was performed by the senior representatives of the Biboki clans. This ceremony is synonymous with a sword and a sheath. The sheath was representative of Ain Le'u's physical body, which was believed to be departing. The sword, representing her soul, was believed to be remaining.

Initially, money was donated and collected in the presence of the 'representative' Ain Le'u and then divided into two bundles known as *buah maputu (BK).* Bracelets were added to each bundle, before they were tied with cloth – one bundle with white cloth and the other with red cloth. These were then attached to either end of a stick along with two longer pieces of cloth similar to pennants, also white and red respectively. These pennants, *katkiti (BK)* (Fig. 11), were to be kept as a remembrance by the family. The white cloth was representative of Ain Le'u's body and was referred to as the 'foot' of the stick. The red cloth represented her soul that was to remain, referred to as the 'head' of the stick. The *katkiti* were prepared by senior men from various clans in front of the representative Ain Le'u, who sat regally, adorned with the red head band, as opposed to the deceased Ain Le'u, who wore a white cloth head band (Fig. 6).

PROCESSION, BURIAL AND PURIFICATION

Once the *katkiti* was prepared, the family bade their final farewell to Ain Le'u and closed the coffin, which was then carried from the house to commence the procession to the graveyard[31]. Her coffin was draped with a hand woven *beti naek*, woven in the warp ikat technique, decorated with a Biboki motif. The white *kain tele* adorned with the crucifix (Fig. 5) was placed on top of this cloth. The procession carrying the coffin was led by Ain Le'u's brother-in-law who carried the *kakiti* pennants and the *buah maputu* tied to the stick. Behind the coffin, mourners dressed in black with loose hair carried large baskets; *bakul (BK)* on their heads, filled with offerings of cloth that had been given to the family by mourners, signifying the respect and familial alliances offered to Ain Le'u and her descendants (Fig. 12). The procession proceeded through a guard of honour formed by the hundreds of mourners until it reached the compound border of the Us Boko residence. Here, in order to signify Ain Le'u's final departure from her home, three gun shots were fired. This act was possibly an adaptation

Fig. 12. Women carrying baskets of hand woven cloth as part of the funeral procession. This cloth had been gifted to Ain Le'u's family by mourners in recognition of clan alliances.

of the tradition of burial in Tamkesi whereby the gong is struck and rings out advising the kingdom of the death of an aristocrat. Then a dog was strung and shot with the intention of ensuring that Ain Le'u would be accompanied by the dog's soul on her journey from that point onward. Following this event, the chief mourners proceeded to the burial site where Ain Le'u was finally interred.

The other mourners slowly returned to the house compound and gathered near the *Ai No'on* fire for the completion of the proceedings for the ceremony that followed. The Kaiser's younger brother was responsible for purifying all the mourners by splashing them with leaves dipped in water gathered from a sacred water source, *oe le'u (BK).*[32] For ceremonial purposes the water for the royal Us Boko clan is collected by a designated person of the Us Kenet clan, who must wear full ceremonial attire when collecting the water. Sacred water is not used at birth, but only at mortuary ceremonies. This enabled the mourners to leave the heated ceremonial state of the funeral ceremony and re-enter the cool state of everyday life and safely resume their journey homeward, avoiding otherwise anticipated danger such as being struck by lightning. Following the completion of the purification ceremony the *Ai No'on* fire was extinguished using a grass, *hun usu (BK)*, *Imperata cylindrical (L)*[33], as these leaves are considered to be the first natural element in creation.

CONCLUSION

It is evident from Ain Le'u's funeral that cloth is used in a variety of contexts in funeral practices in Biboki. Intricate hand woven textiles are used to adorn the deceased and gifted to her with the intention of these finest cloths accompanying her to the afterlife. Her burial attire indicated her high status both through the motif and intricacy of her hand woven tube skirt as well as through the attire resulting from foreign Dutch and Javanese influence. In the instance of the mourners, their attire was tempered by indigenous or possibly Chinese protocol, which prohibited the wearing of red clothes. *Paek metan*, a form of European influence, were worn to indicate the wearer's state of mourning. Chinese protocols determined the use of white attire by the chief mourners, while batik cloth was featured on the priest's vestments.

Hand woven textiles were also gifted and consequently redistributed amongst the family of the deceased as a means of paying homage and reinforcing clan alliances. In the process of mourning, these gifted cloths were used to frame the sacred mortuary space, which was ultimately delineated by a pair of hand woven cloths featuring Biboki motifs (Fig. 2). This pair of cloths, identified as masculine and feminine, was a manifestation of the symbolic dualism that underpins Atoin Meto society. Other representations of this dualism were evident in the complementary opposites of the *katiki*, incorporating the red and white cloths representing the mundane world of the body and the afterlife into which Ain Le'u's soul was being released, as evident in the mortuary practices described. Further dualism was evident in the headdresses worn by the deceased Ain Le'u and the living representation of her, adorned in *meo* attire. Again the duality of red and white cloth headbands indicated the counterparts of existence, life and death, physical and metaphysical. The final gesture of this adherence to complementary opposites, whether consciously done or not, was the placement of the white *kain tele* with the Christian crucifix embroidery over the hand woven warp ikat cloth featuring a Biboki motif on top of the coffin during the funeral procession. These shrouds physically illustrated the co-existence of the indigenous and Christian iconography and associated beliefs.

Through the perspective of Ain Le'u's funeral it has been possible to gain insights into the manner in which textiles uphold customary notions of dualism as well as embodying various cultural influences. Together, these beliefs and influences form a syncretic belief system, which is evident in the contemporary ceremonial practices of the indigenous, aristocratic clans of Biboki people. Furthermore, Ain Le'u's funeral illustrates the dynamic nature of Atoin Meto culture, reminding us that the textile traditions of this culture are not static. By analysing the uses and symbolism attributed to the textiles used at Ain Le'u's funeral, the continued significance of textiles in the formation and expression of Atoin Meto cultural identity, ceremonial practices and religious beliefs is asserted.

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ENDNOTES

1. Ain Le'u was also widely known as *Isteri Kaiser Biboki (I)*. 'Kaiser' was a term introduced into the region by Dutch colonisers. It replaced other terms such as *Neon, Atupas (BK)* and *Raja (I)*.

2. The Kaiser of Biboki is known by several names including: *Koko, Neno Anan, Paha Tuana, Hit Tua Ka (BK)*.

3. In addition to Biboki, the other kingdoms were Amarasi, Amfoang, Fateleu, Amanatun, Amanuban, Molo, Insana, Miamafo and Belu.

4. The origins of the Kingdom's name and the location of Tamkesi are preserved in an ancient story. Some Atoin Meto people were travelling with a horse. This horse carried a *boki (BK)*, a wooden stick balanced across its back for the transportation of goods. When the horse arrived at Tamkesi the *boki* balanced evenly across its back. This indicated to the people that this was a place of special power and so the name Biboki was given to the Kingdom and the site of Tamkesi was chosen as its sacred heart (Ibu M. Y. Meta pers. comm. November 2003, Kefamenanu).

5. The most eastern, male mountain is known as *Bukit Tan Pah*. The western, female mountain is known as *Oepuah*. Together they form *pah-nifu (BK)*; land and water, considered to be a place of origin for Biboki people.

6. Located above Tautpah village to the west, are a series of dwellings including *ume le'u* of the Biboki Kingdom. It has the special name of *panu (BK)* as it is the sacred ceremonial house of Biboki. Nearby the *panu* is the *Lopo Tain Lasi*.

7. The *Neno Biboki* or *Atupas* is the sacral lord of the realm, and as such never leaves the navel centre. *Neno Biboki* can be translated to 'He who sleeps and eats' (Schulte Nordholt 1971: 239–243) provides a detailed description of the ritual centre of Biboki. The current *Neno Biboki* is also known as Klemens Us Boko.

8. Ain Le'u also refers to one who gives coolness and freshness to all she meets.

9. An invitation to attend the funeral was issued by Mrs Yovita Meta, Director of Yayasan Tafean Pah weaving co-operative. Permission to document the occasion was granted by Tnesi Iba Us Boko.

10. As part of the formal funeral proceedings a statement written by the four children of Ain Le'u was read explaining their preference for burying their mother in Kaubele, in the first instance. Following a period of five years, it is their intention that her remains be relocated to Tamkesi. The practice of relocating human remains occurs in cases where people marry into other clans and consequently relocate to a new area. In such instances, the remains of deceased family members along with the objects they are buried with are dug up and then washed before being placed in a small wooden coffin. The services of a specially qualified person are required to perform these tasks and associated rites. This process occurs in a specially allocated place near the burial site. Once the remains are reburied at the new location, a special ceremony is undertaken by the family members in order to invite the spirit of the deceased to follow.

11. At birth, *kusambi* is burnt inside the house, beneath the mother's birthing platform, and kept alight until she and baby emerge after approximately forty days of seclusion. At death, *kusambi* wood is burnt outside the house of the deceased. In both instances the purpose is to heat up the ceremonies and it serves as a protective agent; however, a comparison between the inner realm of life and the outer realm of death is also articulated by this ceremonial fire practice.

12. Nack Le'u clan (Mr Nikolas Bano), Subun clan (Mr Hendrikus Nesi) and Tas Au clan (Mr Tas Au).

13. Groups of guests included relations, neighbouring families, clans, villages, local officials and representatives of community associations, politicians, bureaucrats and school groups.

14. The number seven repeatedly appeared throughout the funeral ceremony including seven strikes of the sene; seven ceremonial breast plates, *noen bena (BK)*, hung at the head of Ain Le'u's coffin; seven strings of *molo* (*molo* are considered to be a friend with *noen bena*), seven ambulations of the dance, *liqurai (BK)*. The significance of seven is attributed to a myth derived from Tamkesi, whereby seven hailstones fell from the sky, inspiring the textile single warp ikat textile motif known as *san sieu no'o* (motif showing the impressions of the hailstones on the land). In response to the dual nature of all things in Biboki, there also exists

a motif known as *san sene* (depicting the seven hailstones). One motif represents the worldly, land based existence whilst the other represents the sky based, unseen, higher forces. This emphasises the notion of keeping seven and returning seven to the gods. i.e. seven for the Gods; seven for the earth/living. (Mr Philipus Manek pers. comm. Kaubele village, Usat Nesi clan, speaker for the Kaiser on sacred matters *Moin Le'u / Atoni Le'u (BK)*.

15. Hair worn loose is also a custom practised in the nearby Belu region where people also avoid wearing jewellery and bathing until after the deceased has been buried. Also in Belu it is noted that men cannot cut their hair or wear head cloth, *pilu (BK)*, during mourning (Yeager 2002: 50).

16. In neighbouring Timor-Leste women observe mourning by wearing a black head scarf, *lutu (T)*, as a sign of mourning.

17. Traditionally coffins were made of wood from the *gewang* palm and *kapok* fibre.

18. Traditionally, it was the Kaiser's wife who had the requisite time and access to materials to produce textiles of the highest quality. Furthermore, it was the Kaiser's wife who had the position to introduce innovation in the textile arts, which were otherwise steadfastly guarded by clan protocols.

19. Bow and arrow is known as *panah dan busu* in Bahasa Indonesian.

20. Also known as *nit none (BK), keke (T)*.

21. Various other gifts such as jewellery, notes and photos were also included.

22. Referred to as *Us Boko mafut Us Finit*, this textile illustrated and reinforced the relationship created by the Kaiser's sister's daughter having married into the royal Us Finit clan of Insana.

23. This *tais ha ma buna* was presented by Yayasan Tafean Pah weaving co-operative based in Biboki. Senior weavers from this organisation were present. Mrs Yuliana Nahas, of the Nahas clan from Sainuip village, South Biboki, presented the cloth on behalf of the co-operative.

24. One of the Nahas women married into the Us Boko clan, directly into the family of the Kaiser of Biboki. Such intermarriage was a result of a successful military campaign mounted by the Kaiser, which the Nahas clan supported. Recognising the support of the Nahas clan the Kaiser bestowed upon them land and a marriage allegiance was formed between the Usboko and Nahas clans.

25. The hand mirror placed inside the coffin had also been broken for this same purpose.

26. Alternatively a set of songs known as *Boin Ma Mean*, songs of happiness, are performed at celebratory occasions, such as *Monet Tok Tan'ni* ceremonies when the newborn child's placenta is buried.

27. In Timor-Leste it can be removed and placed at the burial site where it is simply left to disintegrate (Cecilia Assis pers. comm. 19 Dec 2007).

28. This style of headdress is also known as *tefan* (Coury 2004: 63).

29. Textiles, fertility and head-hunting were traditionally interrelated forming a symbolic triad, with the act of weaving being known as 'the warpath of women' (Howell 1912: 63 cited by Gittinger 1979: 31–32).

30. These skills for life are known as *Monet Tok Tan'ni*. For a boy child a knife, hoe, and *besi kafa (BK)* are the implements used in the ceremony asking that the son be endowed with *fani benas na'ik (BK)*, the ability to sharpen knives and axes, *tua helna na'oe (BK)*, the skill of cutting and milking the lontar palm and *bae'ka (BK)*, the skill of dancing and drumming.

    For a girl child *ike, suti, keo (BK)*, represent the skill of weaving, *kanot (BK)*, the skill of basketry and *bae'ka (BK)*, the skills of dancing and drumming are requested by the family. If she can master these arts she will be blessed with a good life (Barrkman 2007: 75–76). On this occasion the *Bonet Pantun*, a call and response chant is recited, which describes the beginning of the world. (Philipus Manek, Kaubele pers. comm. 18 March, 2006).

31. During funerals conducted at Tamkesi, a large pestle, *esu (BK)*, used for pounding corn, is wrapped with a woven shoulder cloth, *bet ana (BK)*. In this way the *esu* is symbolic of a person being clothed. Otherwise it is like the deceased person remaining naked. The Naik Nahas, Hu Moin and Sikas clans are responsible for attending to the *esu* on these occasions. Usually during a death in the Usboko clan the pestle is wrapped at the time the *Ai No'no* fire is lit. After burial of the corpse the *Ai No'no* fire is extinguished and the bet ana removed from the pestle.

32. Each Biboki clan has two water sources – *oe le'u (BK)*, for sacred water and *oe mata (BK)*, for daily use water.

33. This grass is known as *alang alang (I)* and is used for roofs on traditional domestic dwellings.

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Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) from northern Australia. Family Axinellidae

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ABSTRACT

Nine species in five genera of the family Axinellidae, including three new species, *Axinella loribellae* sp. nov. *A. sinoxea* sp. nov. and *Phakellia tropicalis* sp. nov., are recorded for the tropical northern Australian waters of Western Australia, the Northern Territory and the Queensland coast as part of a revision of the order Halichondrida (Porifera: Demospongiae) in this region. One species, *Dragmacidon durissimum* (Dendy, 1905), generally found in the Indian Ocean, represents a new record for Australia. Taxonomic descriptions and discussion of those species are presented here. The position of *Reniochalina* within the Axinellidae is also discussed based on new evidence found in this and other studies.

Keywords: Sponge, Porifera, Halichondrida, Axinellidae, northern Australia, new species, taxonomy.

INTRODUCTION

The northern marine region of Australia, or the Northern Province as defined by the Interim Marine and Coastal Regionalisation of Australia (IMCRA, version 3.3, www.environment.gov.au/coasts/mpa/imcra/index.html) includes tropical waters off the Northern Territory (from the Admiralty Gulf in the west) and the Queensland coasts (western coast of Cape York to Torres Strait in the east). The continental shelf of this area is generally shallow (less than 70 m) and extensive, reaching approximately 400 km in width in the Timor Sea and adjoining the coast of New Guinea in the Arafura Sea and Torres Strait (Bunt 1987; Ferns 1999). The area is part of the central Indo-West Pacific, which is well known for its high species-richness, high levels of endemism and is considered to be centre of origin of many tropical marine species (Veron 1995).

Sponges are one of the most diverse and prevalent groups of marine invertebrates of northern Australia, but also one of the most poorly known in terms of proportions of known and new species, and levels of endemism. According to Hooper *et al.* (1997) the northern sponge fauna includes approximately 800 species, 60% of which remain undescribed. Further studies based on 'presence-absence' analyses of the diversity of tropical Australian sponges (Hooper *et al.* 2002) identified at least two 'hot spots' of biodiversity for the northern area, one in the region of Darwin and Cobourg Peninsula and the other in the Wessel Islands region. Only 30% of the sponge species included in that biodiversity study could be assigned to a known taxon indicating that a great percentage of the fauna of that region is not well known.

Taxonomic knowledge of northern Australian sponges is limited to a few studies. The first sponges collected from this area were described by Ridley (1884) and included 24 species, of which only 17 are currently recognised as valid species. Bergquist and Tizard (1967) later described 19 species from the rich intertidal area of Darwin Harbour. Since 1967, there have been 50 additional records to the fauna of northern Australia and only one revision of a particular group, i.e. the family Halichondriidae (Hooper *et al.* 1997 and references within). Recent descriptions of some species have also been included in major taxonomic revisions of the demosponge families Raspailiidae (Hooper 1991) and Microcionidae (Hooper 1996).

The order Halichondrida is presently represented in northern Australia by 41 nominal species (Hooper and Wiedenmayer 1994; Hooper *et al.* 1997), and a large number of specimens recently collected and deposited in the Museum and Art Gallery Northern Territory and the Queensland Museum (see abbreviations below). Data gathered from these collections clearly indicate that new species and records are represented in the area, and that species previously recorded also need to be revised using more sophisticated taxonomical tools.

The Halichondrida is a group with an uncertain classification and definition. As with many other sponge groups, it is defined by traditional morphological characters, such as growth form, surface characteristics and skeletal features. But in the Halichondrida, however, these characters are extremely simple, polymorphic and few, and as a consequence the discrimination of taxa within this group is ambiguous. Halichondrid sponges have diverse growth forms (e.g. encrusting, massive, ramose, tubular, flabellate).

The skeletons are plumoreticulate, dendritic or confused, constructed with three types of spicules (strongyles, styles and oxeas), or transitional forms, in any combination and not functionally localised. The order includes five families (Axinellidae, Dictyonellidae, Heteroxyidae, Halichondriidae and Bubaridae), and 45 genera, most of which remain poorly defined despite recent efforts to clarify and redefined the taxonomy of these families (Alvarez and Hooper 2002; Alvarez and Van Soest 2002; Hooper 2002a; Van Soest *et al.* 2002; Van Soest and Hooper 2002). Evidence from molecular studies (Alvarez *et al.* 2000) indicates also that some of the genera are not monophyletic. Moreover, species allocated to some genera (e.g. *Axinella*, *Acanthella*, *Phakellia*) have fuzzy boundaries and overlapping characters and include numerous forms (or varieties/morphs). Similarly, some allegedly widely distributed species may represent complexes of cryptic species hiding under morphotypes that span a continuum, and which cannot be resolved easily using morphometric data alone.

The taxonomic confusion around the Halichondrida, has generated long-lasting debates at higher levels of sponge classification. Further studies using larger groups of species, revisions at the regional level and different kinds of genetic and chemical approaches have been recommended to refine the current concept of this taxon (Van Soest and Hooper 2002).

The aim of this study is to revise the fauna of the Halichondrida from northern Australia and the status of all the nominal halichondrid species in this region. The present paper represents the first part of this revision and includes the family Axinellidae. Revision of the remaining families represented in the area (i.e. Dictyonellidae, Halichondriidae and Heteroxyidae) will follow in separate papers.

MATERIALS AND METHODS

This revision includes material of the family Axinellidae recorded for the tropical northern Australian waters of the Western Australia, Northern Territory and Queensland coast (from Admiralty Gulf in the west to Torres Strait in the east, approx. between the 125° E and 142° E meridians (Fig. 1). The area does not represent a true biogeographical area and it was delimited based on the marine bioregions defined by IMCRA. This area also corresponds with two of the ecoregions (i.e. Arafura Sea, Arnhem Coast to Gulf of Carpenteria) of the Sahul Shelf marine province as defined by Spalding *et al.* (2007).

All specimens recorded for the selected area and registered under Axinellidae at the Queensland Museum and the Museum and Art Gallery Northern Territory sponge collections were examined and identifications were verified. Specimens and relevant type material from adjacent areas including western Australia, the Ashmore, Cartier and Hibernia reefs on the Sahul Shelf, Lesser Sunda Islands, Aru Islands, the south coast of Papua New Guinea and Great Barrier Reef were also examined if the species distribution was included in the studied area.

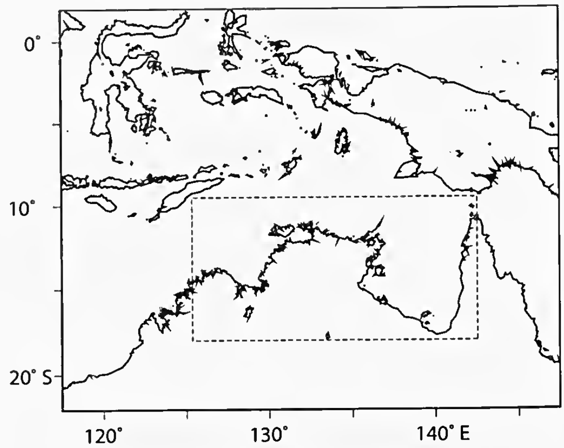

Fig. 1. Study area included in this taxonomic revision.

Complete locality and collection data of material included in this revision is indicated under the species description as usual, whereas non type voucher material deposited at the Queensland Museum and the Museum and Art Gallery Northern Territory, is listed in Appendix 1.

Specimens were prepared for light microscopy using the usual methods (e.g. Hooper 1996; Van Soest and Hooper 2005). Spicule measurements are in micrometres, based on 25 spicules (otherwise indicated in brackets), of each category and denoted as range (and mean ± 1 S.E.) of spicule length x spicule width. Measurements were made using a digital video camera attached to a light microscope in combination with the software V++ Precision Digital Imaging System v 4.0 (© Digital Optics Ltd). Scanning Electron Microscope photographs were taken in a JEOL JSM 5610LV. The higher systematic arrangement follows classification in the current version of World Porifera Database (Van Soest *et al.* 2008).

Terminology used here follows Boury-Esnault and Rützler (1997) and Alvarez and Hooper (2002).

ABBREVIATIONS

Abbreviations used in the paper are: AIMS, Australian Institute of Marine Sciences; BMNH, Natural History Museum, London (formerly British Museum Natural History); CRRF, Coral Reef Research Foundation, Palau; GBR, Great Barrier Reef, NTM, Museum and Art Gallery Northern Territory, Darwin, Australia (formerly Northern Territory Museum); MONZ, Museum of New Zealand; NTM, Museum and Art Gallery Northern Territory (formerly Northern Territory Museum), Darwin; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt; QLD, Queensland, Australia; QM, Queensland Museum, Brisbane; WA, Western Australia,

Australia; ZMA, Zoologisch Museum, University of Amsterdam, Amsterdam.

Numbers prefixed with Q666C, 0CDN, 0M9H are the cross-reference sample number collected for the United States National Cancer Institute, under the 'Collection of shallow-water organisms' program, by the Australian Institute of Marine Sciences, CRRF and NTM (subcontracted through CRRF), respectively.

TAXONOMY

Order Halichondrida Gray, 1867
Family Axinellidae Carter, 1875

Nine species of Axinellidae, listed below, were recorded within the studied area; three of these being new species.

Axinella aruensis (Hentschel, 1912)
Axinella loribellae sp. nov
Axinella sinoxea sp. nov
Cymbastela stipitata (Bergquist and Tizard, 1967)
Cymbastela vespertina Hooper and Bergquist, 1992
Dragmacidon australe (Bergquist, 1970)
Dragmacidon durissimum (Dendy, 1905)
Phakellia tropicalis sp. nov.
Reniochalina stalagmitis Lendenfeld, 1888

Genus *Axinella* Schmidt, 1862

Gender feminine. Type species, by subsequent designation of De Laubenfels (1936), *Axinella polypoides* Schmidt, 1862. Recent, Adriatic Sea.

Axinella aruensis (Hentschel, 1912)
(Figs 2 A–F, 3, 4, Table 1)

Phakellia aruensis Hentschel, 1912: 420; Hooper *et al.* 1992 [in part]; Pulitzer-Finali 1993: 283.

Axinella aruensis. – Hooper and Wiedenmayer 1994:72; Alvarez *et al.* 2000 [form II, see below]; Alvarez, Krishan and Gibb 2007[form II]; Holmes and Blanch 2007.

Material examined. The material examined for this species is separated according to the morphotypes described below. Holotype – SMF 953, E side, Aru I., Indonesia, 31 August 1908, coll. Merton, H.. Additional specimens – Lacepede Is, NW Shelf, WA: NTM Z.2284, Z.2304, Z.2331, Z.2345. Joseph Bonaparte Gulf: QM G301197, Cartier I.: QM G301092. Melville I. NT: NTM Z.615,

Table 1. Comparison of spicule dimensions among specimens and varieties of *Axinella aruensis*. Measurements in micrometres.

Specimen	Locality	Oxeas	Styles
Axinella aruensis			
SMF 953	Aru Is, Indonesia	257.1–423.9 (360.6±38.1) x 13.8–21.4 (16.5±1.9)	249.1–382.2 (313.6±40.7) [12] x 14.1–21.7 (17.4±2.2) [12]
Z.2304	Lacepede Is, WA	245.5–337.6 (285.4±21) x 8.6–17.2 (13±2.6)	213.2–271.4 (244.8±20.9) [9] x 11.9–15.7 (13.5±1.6) [9]
G301092	Cartier Is, WA	281.2–450.2 (360.7±39.9) x 10.3–19.4 (15.6±2.2)	242.8–419 (301.1±36) x 12.6–20.3 (16.8±1.9)
Z.619	Melville I., NT	236.1–406 (302.4±39.4) x 9.3–17.5 (13.9±2.3)	186–362.8 (267.2±43.3) [22] x 9.8–17.1 (14.1±1.9) [22]
Z.3141	Parry Shoals, NT	267.1–372.9 (307.1±23.3) x 9.4–17.2 (13.6±2.3)	248.6–294.6 (270.4±18.8) [4] x 11.1–16.7 (13.9±2.3) [4]
Z.5053	Darwin Harbour, NT	297.6–498.6 (392.1±47) x 7.3–22.5 (16.5±3.7)	263.6–417.2 (342.7±37.6) x 12–23.5 (17.1±2.9)
Z.4465	Wessel Is, NT	194.4–396.4 (299.5±48.6) [24] x 5.6–17.4 (12±3.3)	204.6–331.7 (269.7±44.1) [15] x 8.6–18 (13.8±2.8) [15]
Axinella aruensis form I			
Z.5816	Bynoe Harbour, NT	305–451.7 (376.7±36.3) x 13.1–25.9 (18.3±3.9)	283.1–406.6 (334.7±40.7) [6] x 14.7–19.6 (16.5±1.8) [6]
Z.3068	Parry Shoals, NT	187.1–318.2 (237.2±26.6) x 8.5–17.2 (13.2±2.4)	167.2–222.5 (200±15.3) x 9.3–15.5 (13.2±1.7)
Z.5819	East Point, Darwin, NT	266.7–354.5 (312.1±23.3) x 13.1–18.8 (16.3±1.4)	200.1–353.2 (260.7±34.1) x 10.3–22.8 (15.4±2.9)
Z.3946	Wessel Is, NT	274.8–392.8 (333±32.8) x 8.3–16.4 (13.3±2.3)	248.6–363.3 (297±31) [10] x 11.5–18 (15.1±2.3) [10]
Axinella aruensis form II			
Z.4490	Stevens Rock, Darwin	209.1–278.6 (246.3±15.8) x 12.7–19.9 (15.1±1.8)	163.6–231.4 (191.1±17.4) x 6.5–12.5 (9.8±1.6)
Z.5054	Wessel Is	173.8–247.4 (214.7±18.9) x 7.5–16.7 (10.3±1.9)	166.4–262.3 (218.2±22.4) x 7.8–17.9 (13.9±2.4)

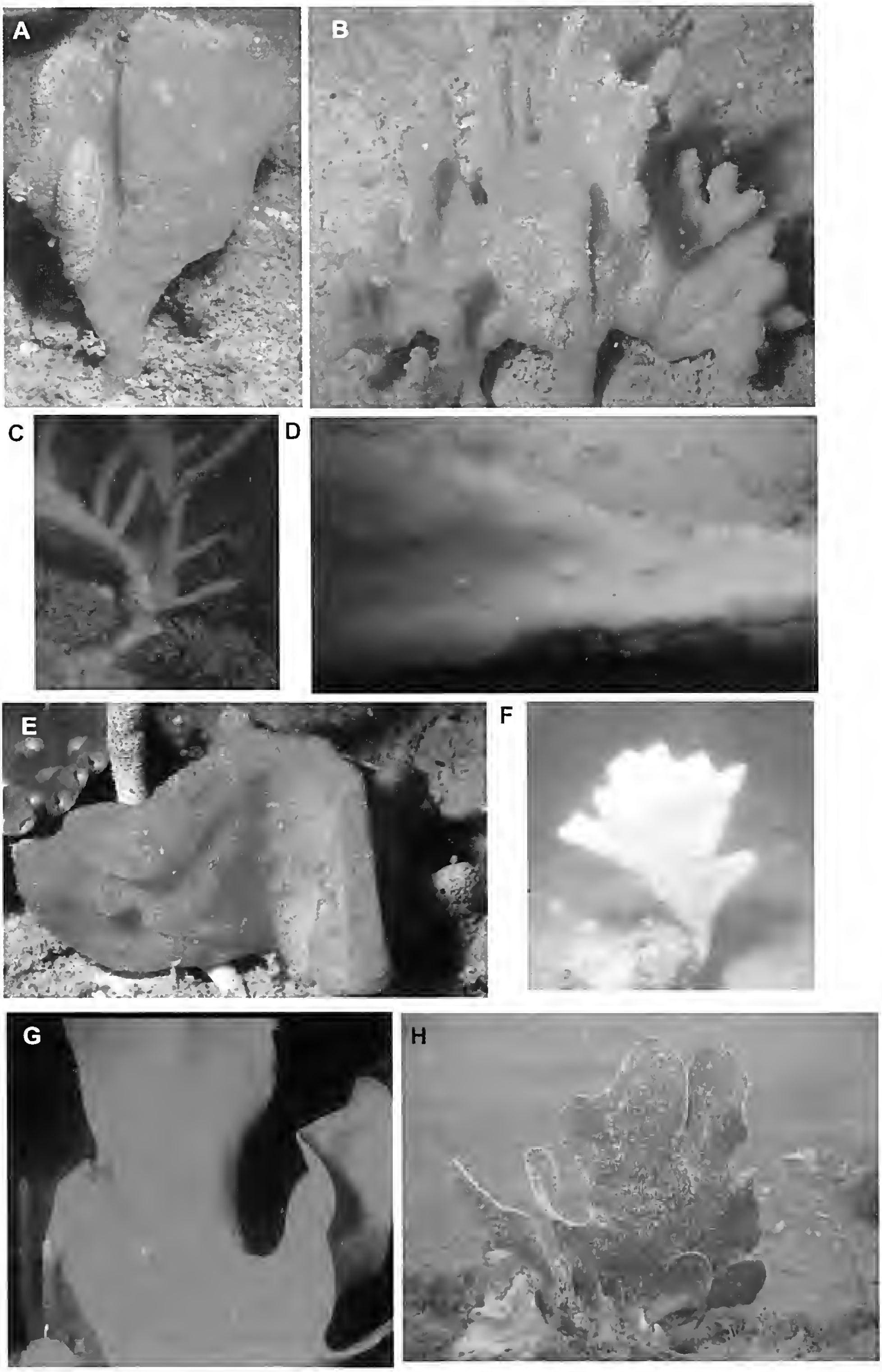

Fig. 2. *Axinella aruensis*: **A, B**, specimens at Raragala I., Wessel Is; **C**, specimen at South Shell I., Darwin Harbour; **D**, form I, Z.5816, Dawson Rock, Bynoe Harbour; **E**, form II, specimen at Raragala I, Wessel Is; **F**, *Axinella sinoxea* sp.nov., NTM Z.2719. *Axinella loribellae* sp. nov.; **G**, Holotype, NTM Z.4427; **H**, NTM Z.5662. Photos: **A–B**, P. Colin; **C–D, G**, B. Alvarez; **E**, D. DeMaria; **F**, J. Hooper; **H**, A. Ayling.

Z.619, Z.630, Z.632. Parry Shoals, Arafura sea, NT: QM G310136 (Q66C0514-X), NTM Z.3062 (Q66C87-0514-X), Z.3141.Bynoe Harbour, NT: NTM Z.5071 (0M9H2464-U). Darwin Harbour, NT: NTM Z.5053 (0M9H2168-X), Z.5057 (0M9H2665-O), Z.5058 (0M9H2675-Y), Z.5072 (0M9H2579-U), Z.5830. Cobourg Peninsula, NT: NTM Z.1363, Z.1388, Z.2511, Z.2526, Z.2529. English Company Is., NT: NTM Z.3956. Wessel Is, Gove Peninsula, NT: QM G3.609 (Q66C4762-R), G300768 (=Q66C4737P, QM G311873 and NTM Z.3945), Z.3922 (Q66C4687-L), Z.3935 (=Q66C4785-R, QM G300752), Z.3936 (Q66C4831-R), Z.4465 (0M9H2770-C), Z.5055 (0M9H2650-W). Papua New Guinea: QM G312913, G312935.

Axinella aruensis, form I, Bynoe Harbour, NT: NTM Z.5816, Z.5817, Z.5818. Darwin Harbour, NT: NTM Z.2156, Z.5819-Z.5823. Wessel Is, Gove Peninsula, NT: NTM Z.3925, Z.3946.

Axinella aruensis, form II. Darwin Harbour, NT: QM G303332, Z.1961, Z.2249, Z.2402, Z.2632, Z.4425 (0M9H2044-O), Z.4490, Z.4491, Z.5824-Z.5829, Z.5831, Z.5232. Parry Shoals, Arafura sea, NT: NTM Z.3137, Z.3068. Wessel Is, Gove Peninsula, NT: QM G300759 (Q66C-4831-R), NTM Z.5054 (0M9H2648-U). Yampy sound, WA, NTM Z.665.

Description. Three different morphotypes of this species with one corresponding to the holotype are recognisable among the material examined and they will be described below separately under the heading of 'forms'.

***Axinella aruensis*, typical form.** *Shape* (Fig. 2A–C). Thickly flabellated, on broad and short, or long and narrow, peduncle, uni or bi-planar, sometimes folded, with round margins projecting in most cases into short and broad extensions with square, round or pointed tips, or in long rounded to flat branches which tend to fuse laterally. Specimens up to 400 mm high.

Colour. Orange, pale yellow or yellowish brown alive. Dark brown in alcohol.

Oscula. Regularly distributed in one or both sides of fan, stellate, flush or with elevated rims, less than 5 mm diameter.

Surface. Evenly microconulose-conulose, nodulose, rough, marked with primary longitudinal choanosomal fibres.

Skeleton (Fig. 3A). Plumose, vaguely reticulated to halichondroid, very compact, with plumose columns up to 600 µm thick, diverging toward surface, ending in fan-shapped spicule brushes and projecting through ectosome. Axial skeleton differentiated only towards base of attachment or peduncle, halichondroid.

Spicules (Fig. 3B). Oxeas with blunt, pointed or telescoped tips; slightly bent and sometimes slightly sinuous, 195–498 x 5–22 µm. Styles, less frequent or rare, similar in size to oxeas (see Table 1) with blunt ends, enlarged or slightly narrow bases, straight or slightly bent. Transitional forms (e.g. styloids, strongyles) are common.

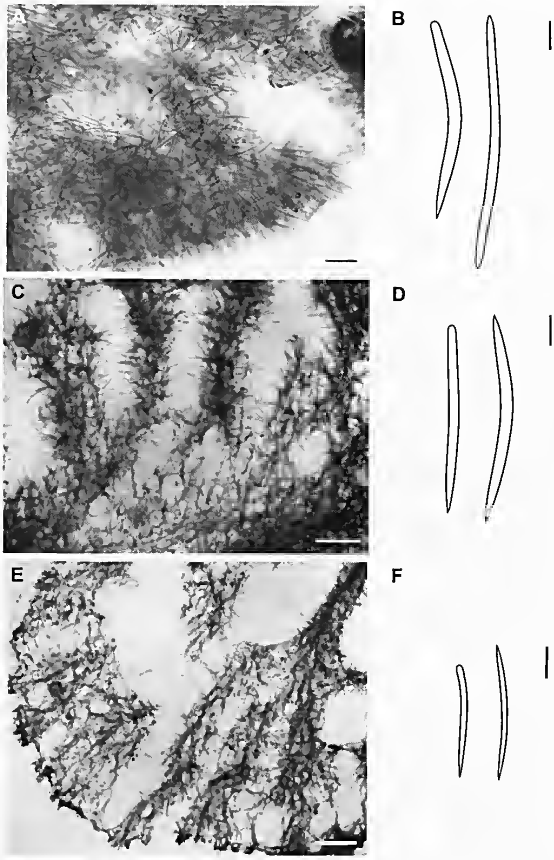

Fig. 3. *Axinella aruensis*: light microphotograph of skeleton and diagram of spicules: **A, B**, SMF 953, holotype; **C, D**, Z.5819 (form I); **E, F**, NTM Z.5054 (form II). Scale bars: **A**, 200 µm; **B, D, F**, 50 µm; **C, E**, 500 µm.

***Axinella aruensis*, form I.** *Shape* (Fig. 2D). Erect, fan-shaped or narrow long and flat digits with few simple ramifications, generally with square margins. Specimens up to 20 cm high and 10 cm wide.

Colour. Light orange, brown, beige or yellow. Same colour in alcohol.

Oscula. Regularly distributed, less than 5 mm diameter, with distinctive raised margins.

Surface. Minutely hispid, marked with choanosomal skeletal tracts in a regular reticulation or with radial grooves.

Skeleton (Fig. 3C). Plumose and slightly compressed at axial region, with thick plumo-echinated multispicular columns, up to 1 mm thick, and radiating outwards towards surface, anastomosing or connected irregularly by short and thick paucispicular or multispicular tracts, or by single spicules oriented in any direction. Main tracts end at surface in fan-shaped brushes with spicules projecting shortly through ectosome; light spongin embedding tracts.

Spicules (Fig. 3D, Table 1). Oxeas, 187–451 x 8–25 µm, with pointed or blunt ends, straight or bent; thinner forms are common. Styles less frequent or rare, slightly smaller,

including intermediate forms similar to styloids, anisoxeas or strongyles. Fused spicules are characteristically common.

***Axinella aruensis*, form II.** *Shape* (Fig. 2E). Thick fans or lamellae with round margins, folding in more than one perpendicular plane, or joining at angles from 45-90 degrees; or short single or digitate projections, stipitate, on short narrow peduncles or on broad base. Generally small with individuals reaching up to 13 cm high.

Colour. Bright or light orange alive. Light beige in alcohol.

Oscula. Stellate with minute drainage canals, sometimes located at margin of fans or evenly distributed in both sides of fan, 3-5 mm in diameter.

Surface. Pierced uniformly with minute ostia. Microconulose; minutely hispid, firm but some has mucous consistency after collection. Marked by regular choanosomal reticulation.

Skeleton (Fig. 3E). Thick and dense plumo-echinated multispicular tracts up to 600 µm wide, forming regular, nearly radial reticulation which is marked on surface. Main columns end at surface in fan-shaped brushes, with spicules projecting shortly through ectosome. Axial skeleton not differentiated.

Spicules (Fig. 3F, Table 1). Oxeas and styles in nearly equal proportions, 174-279 x 7-20µm. Styles are dominant and slightly smaller than oxeas.

Remarks. Although some features allowed distinction of two additional morphotypes within this species, the limits among them are not clear and some individuals could be considered intermediate forms. *Axinella aruensis sensu stricto* is distinguished from its two other forms by shape and colour, generally observed to be thickly flabellate and orange when alive, by the change of colour in alcohol (it turns brown) and by the dominance of oxeas in relation to styles. Form I differs slightly in shape from *A. aruensis*; the colour in life is always beige or pale yellow and does not change in alcohol; oxeas are also dominant and styles are relatively more common. Form II is always beige in alcohol and styles are dominant relative to oxeas. Some other features of shape and surface consistency and texture are also distinctive within this form.

Some data included in Hooper *et al.* (1992) indicate there are some differences in the biochemistry between populations (i.e. North West Shelf versus Darwin Harbour) of this species, however the published results do not seem to be related to the forms distinguished here.

Alvarez *et al.* (2007) detected up to 29% of intra-genomic polymorphism within the Internal Transcribe Spacer (ITS) of the rDNA in individuals of *Axinella aruensis* from Darwin Harbour. These levels of intra-genomic variation are so far the highest reported for Porifera and correspond in most cases to hybrid species reported for other groups, including corals of the genus *Acropora*. Thus, it is possible that the forms here distinguished to document the variability present within species are the result of a hybridisation processes with sympatric species or populations. Future population genetic studies will help to determine whether the variability observed across these forms are significant to justify their recognition as different species or as hybrids.

Axinella aruensis is very similar in shape, skeletal architecture and spicule composition and dimensions to some *Axinella* species recorded from the Indian Ocean (e.g. *A. donnani* (Bowerbank, 1873); *A. manus* Dendy, 1905 and *A. symmetrica* (Dendy, 1905, as *Phakellia*)). Skeletal reticulation of the Indian Ocean species, in particular *A. donnani*, is much more regular, with thicker primary lines. Interesting also is the change in colouration, from orange to brown after few hours of collection, reported for *A. donnani* (Bowerbank, 1873), a characteristic also seen in *A. aruensis*. A detailed revision of the Indian Ocean species complemented with population genetic studies is essential to define their limits and phylogenetic relationships with the northern Australian populations of *A. aruensis* and its forms.

Distribution. *Axinella aruensis* and its forms appear to occur sympatrically and are common throughout northern Australia (Fig. 4). The type locality is the Aru Is, Indonesia, but the species is also known from other Indonesian localities (Alvarez and de Voogd, unpublished data) and from Papua New Guinea. It is found in subtidal areas from 5 to 76 m. Pulitzer-Finali's (1993) record for East Africa, is dubious and requires confirmation.

Axinella loribellae sp. nov
(Figs 2G–H; 5)

Material examined. Holotype – NTM Z.4427 (0M9H2041-L), Stevens Rock, Weed Reef, Darwin Harbour, 12°29.2001'S, 130°47.1'E, NT, 5–19 m depth, 8 May 2002, coll. B. Alvarez and party. Paratypes – NTM Z.5834 Stevens Rock, Weed Reef, Darwin Harbour, Northern Territory, Australia, 12°29.1667'S, 130°47.19'E, 17 m depth, 8 May 2006, coll. B. Alvarez.

Additional specimens. Melville I., NT, NTM Z.631. Darwin Harbour, NT: QM G303388, NTM Z.822, Z.868, Z.5662. Wessel Is, NT: NTM Z.3938, Z.5059 (0M9H2771-F).

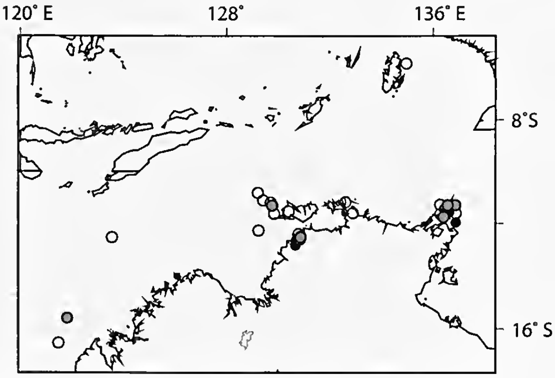

Fig. 4. Distribution of *Axinella aruensis* (open circles) and its forms (I, black circles; II, grey circles) based on confirmed records from QM and NTM.

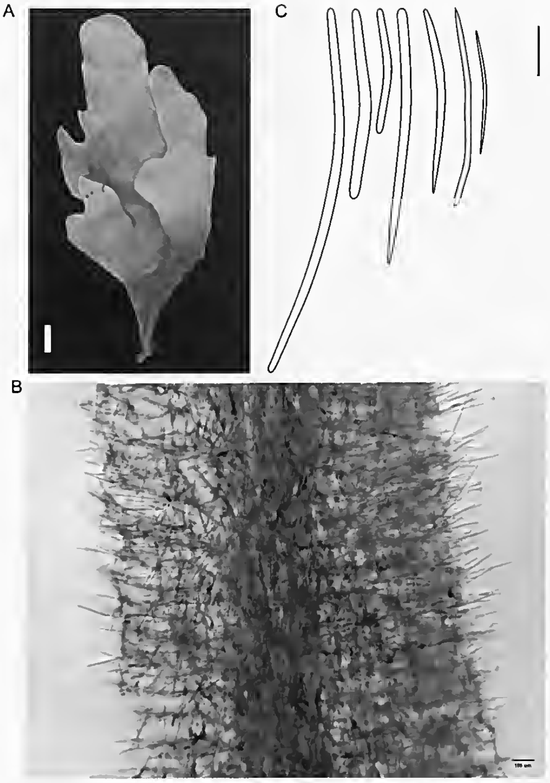

Fig. 5. *Axinella loribellae* sp. nov.: **A,** Paratype, NTM Z.5834; **B,** light microphotograph of skeleton; **C,** diagram of spicules. Scale bars: **A,** 2 cm; **B,** 100 µm; **C,** 50 µm.

Description. Shape (Figs 2G–H, 5A). Fan-shaped; thin lamellae, 1–5 mm thick, single or bifurcated, sometimes convoluted with rounded margins and indentations on short stalks or broad base. Specimens are 300 mm high and up to 400 mm wide.

Colour. Burnt orange alive, brown in alcohol.

Oscula. Small, 2–5 mm diameter, with stellate drainage canals, evenly distributed.

Consistency. Flexible, easy to tear, rubbery.

Surface. Smooth, velvety, marked irregularly with ribs.

Skeleton (Fig. 5B). Plumose, differentiated in extra-axial and axial region. Axial skeleton compressed with wavy longitudinal paucispicular-multispicular tracts, lightly embedded in collagenous spongin, interwoven, and radiating towards the extra-axial region. Extra-axial region a close-set reticulation of plumose paucispicular tracts oriented perpendicular to surface and laterally close, connected by single spicules or uni-paucispicular tracts up to 2 spicules long, cemented with thin and clear spongin, to each other and ending in brushes of spicules that protrude shortly through ectosome.

Spicules (Fig. 5C; Table 2). Styles slightly bent; strongyles straight, slightly sinuous, bent in middle; oxeas fusiform, straight. Transitional shapes between monoactins and diactins are common. All types in a wide range of sizes and thickness. Dominant types vary among specimens (see below).

Remarks. A great variability in the shape and size of spicules was observed among specimens of this species. Styles and strongyles of 190–270 by 7–13 µm, are the dominant types, however they were absent in some of the examined specimens (i.e. NTM Z.631 and NTM Z.3938). Apart from these differences in spicule composition and dimensions, no other characters seem to vary among specimens examined here, and consequently they are considered at this stage to belong to a single species. Further genetic studies may help to confirm whether or not variability in spicule dimensions and composition is indicative of sibling species differentiation.

The new species differs from *Axinella aruensis* and its related species from the Indian Ocean (see above) mainly in shape (thinly instead of thickly flabellate); in skeletal architecture (clearly differentiated into axial and extra-axial skeleton with thinner extra-axial spicular tracts and more regular reticulation when compared to the thicker multispicular columns present in *A. aruensis*) and in spicule composition (with common transitional shapes between oxeas and styles not observed in *A. aruensis*).

Axinella ceylonensis (Dendy, 1905, as *Phakellia*) from the Gulf of Manaar is similar to *A. loribellae* in shape (although shortly stipitate) and in thickness of the lamellae. Both species share the variability observed in the size and shape of oxeas and styles. The two species differ in skeletal and surface characteristics. The skeleton of *A. ceylonensis* is not differentiated in axial and extra-axial region but described as plumose, with columns radiating outwards into small surface conules. No other species in the study area or in the Indian Ocean is similar to this new species. Indeed, most nominal species of *Axinella* reported for the Indian Ocean, do not agree with the current diagnosis of the genus and need to be re-examined. Some of these are massive forms with styles and trichodragmata in the skeleton and might belong in the axinellid genus *Dragmacidon* (e.g. *Axinella*

Table 2. Comparison of spicule dimensions among specimens of *Axinella loribellae* sp. nov. Measurements in micrometres.

Specimen	Locality	Styles	Strongyles	Oxeas
Z.4427 (Holotype)	Darwin Harbour	196.3–352.9 (274.6±47.7) x 8.33–18.3 (13.5±2.7)	103.6–396.3 (190.1±74.0) x 6.01–13.09 (10.3±1.9)	148.5–440.2 (226.8±63.6) x 4.8–12.9 (8.7±2.1)
Z.5059	Wessel Is	159.7–365.4 (250.6±50.4) x 5.8–14.43 (10.0±2.1)	93.7–531.8 (243.1±128.6) x 5.8–13.3 (8.8±2.3)	100.8–302.2 (208.5±50.1) x 3.7–11.4 (6.5±2.1)
Z.631	Melville Is	187.6–307.9 (228.9±29.0) x 4.3–11.3 (7.3±1.8)	– –	142.8–351.6 (217.8±44.1) x 3.5–13.2 (7.1±2.7)

bidderi Burton, 1959 and *A. massalis* Burton, 1959). Some others are *Stylissa*-like, or other dictyonellid genera, with the surface marked by ridges or conules and with a dense and irregular skeleton of multispicular tracts of styles (e.g. *Axinella bubarinoides* Dendy, 1922; *A. dragmaxioides* Burton, 1959 [?]; *A. flabelloreticulata* (Burton, 1959); *A. labyrinthica* Dendy, 1889; *A. minor* Thomas, 1981; *A. proliferans* Ridley, 1884; *A. tenuidigitata* Dendy, 1905; *A. ventilabrum* Burton, 1959), or closer to halichondrid genera (e.g. *Axinella halichondrioides* Dendy, 1905, which is encrusting and has only oxeas) or to the raspailiid genus *Ceratopsion* (i.e. *Axinella lamellata* Dendy, 1905, with a dermal and tangential layer of small oxeas).

Distribution. *Axinella loribellae* seems to be restricted to northern Australia between Darwin Harbour and the Wessel Is. It is found between 11–32 m depth.

Etymology. Named after Lori Bell, Coral Reef Research Foundation, Palau, for her considerable contribution to the knowledge of Indo-Pacific sponge diversity and distribution. It is intended as a noun in apposition.

Axinella sinoxea sp. nov.

(Figs 2F, 6A–D)

Material examined. Holotype – NTM Z.940, East Point, Darwin Harbour, NT, 12°24.05′S, 130°48.01′E, 12 m depth, 13 September 1982, coll. Hooper, J.N.A. Paratypes – Z.5833, East Point, Darwin Harbour, NT, 12° 24.484′S, 130° 48.471′E, 11 m depth, 7 June 2007, coll. B. Alvarez.

Additional specimens. NW Shelf, WA: NTM Z.2310, Z.2322. Darwin Harbour, NT: NTM Z.2246, Z.2719.

Description. *Shape* (Figs 2F, 6A). Single or multiple fans, 4–6 mm thick, 8–14 cm long and up to 30 cm wide, on common stalk, 3–5 cm long and 7–10 mm in diameter; erect, uniplanar with digitate to irregular margins or bifurcate tips.

Colour. Orange, pale yellow or beige with light pink tinge alive; brown-grey in alcohol.

Oscula. Regularly distributed in one or both sides of fan, round to elongated or irregularly shaped, some stellate, with slightly elevated rims, less than 1 mm diameter.

Consistency. Soft, floppy, flexible, slightly compressible.

Surface. Smooth but slightly rough to touch; pierced regularly by minute pores, microhispid due to projections of brushes of choanosomal spicules. Encrusted irregularly with detritus in some specimens.

Skeleton (Figs 6B-C). Plumoreticulated, with ascending multispicular tracts connected regularly by single spicules or unispicular tracts, 1 or 2 spicules long, ending in brushes at surface; slightly compressed in axial region. Spicule tracts bound only slightly with clear collagenous spongin.

Spicules (Fig. 6D; Table 3). Styles robust, bent, or less often, straight, enlarged in the middle section, 159–245 x 7–17 µm; thinner category, 97–201 x 2–6 µm also present. Long thin raphids abundant. Smaller oxeas and thick and short strongyles, very rare.

Remarks. This species conforms in most of its characteristics with the current concept of *Axinella*. The absence or low frequencies of oxeas observed in the examined specimens are also seen in other Caribbean species of the genus (e.g. *Axinella waltonsmithi* (de Laubenfels, 1953) and *A. pomponiae* Alvarez, Van Soest and Rützler, 1998), which might be considered a common feature among *Axinella* species.

The new species resembles *Axinella aruensis* in gross morphology and as such can be easily mistaken for it in the field; both are fan-shaped on a common stalk and both have a similar surface pierced with minute ostia and microconulose. But *A. sinoxea* is clearly different from *A. aruensis* in skeletal architecture and spicule composition, having a regular plumoreticulated skeleton of ascending tracts and long thin raphids in the skeleton. As is the case with *A. loribellae*, no other species recorded in the study area or in the Indian Ocean was found to be related to *A. sinoxea*.

Distribution. Common in the vicinity of East Point Sponge Gardens, Darwin Harbour, but also found in deeper waters (down to 40 m) of Western Australia.

Etymology. Latin, *sine*- without; *sinoxea* referring to the lack of proper oxeas characteristic of the species. It is intended as a noun in apposition.

Remarks on *Axinella*. *Axinella* is a widespread genus of sponges with approximately 100 accepted species (Van Soest *et al.* 2008), many of which, however, need to be verified against the current definition of the genus (Alvarez and Hooper 2002). Ongoing revisions of species of *Axinella* and related genera by one of the authors (BA) are undertaken on a regional basis with the purpose to verify the identity of the reported species and the monophyly of the genus, which is currently proven as polyphyletic based on molecular studies (Alvarez *et al.* 2000; Erpenbeck *et al.* 2005).

Three species of *Axinella* (*A. aruensis*, *A. loribellae*, *A. sinoxea*) are reported in this work. No other species of the genus, as far as we know, have been reported within the area of northern Australia that is the subject of this present study. *Axinella echidnaea* reported by Ridley 1884 is accepted as *Reniochalina stalagmitis* (see below).

Table 3. Comparison of spicule dimensions among specimens of *Axinella sinoxea* sp. nov. Measurements in micrometres.

Specimen	Locality	Thick styles	Thin styles	Raphids
Z.940 (Holotype)	East Point, NT	184.5–245.1 (223.7±12.92) 7.35–17.4 (13.11±2.49)	97.77–201.3 (179.64±22.84) [23] x 2.48–5.6 (3.8±1) [23]	192.9–249.6 (227.2±14.9) x 0.8–3.0 (2.0±0.6)
Z.2310	NW Lacepede Is WA	153.4–197.6 (183.4±10.2) x 7.8–12.2 (10.2±1)	131.3–191.2 (152.1±14.8) x 2.2–6.4 (4.4±1.)	131.9–258.6 (201.5±35.1) x 0.37–2.69 (1.6±0.5)

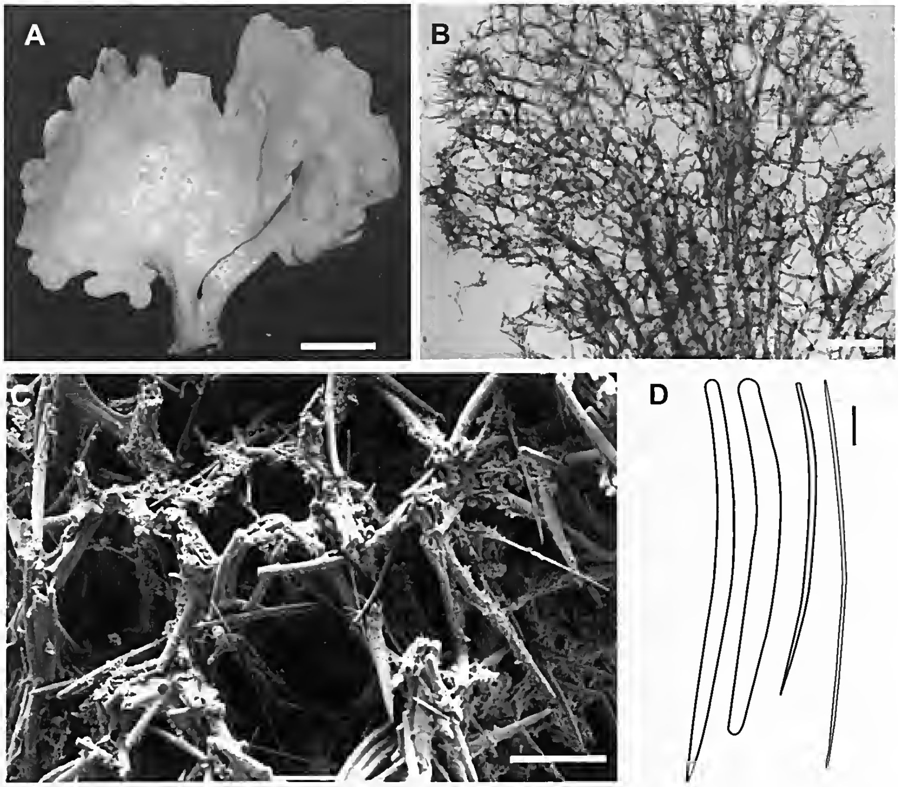

Fig. 6. *Axinella sinoxea* sp. nov. NTM Z.940: **A,** photograph of the holotype; **B,** light microphotograph of the skeleton; **C,** SEM, raphids in choanosomal skeleton; **D,** scale bars: **A,** 5 cm; **B,** 500 µm; **C,** 100 µm; **D,** 20 µm.

In the present study area, the genus *Axinella* seems to be less speciose than in other taxonomically revised regions: seven species in the Western Central Atlantic (Alvarez *et al.* 1998); six (recorded) species and nine possible new species (Kelly *et al.* 2009); at least five species in Indonesia (Alvarez and De Voogd, unpublished data). Unfortunately little is known about the biology of these species to explain why the genus might be more diverse in some areas than others. Many more putative *Axinella* species are known for the GBR (pers. obs.), but these remain unresolved pending future studies.

Distinction of *Axinella* species continues to be subjective and is based on a combination of characters as discussed by Alvarez *et al* (1998). Variability and plasticity of all the morphological characters that characterise the species are seen in all the species described above. The morphological variability of *A. aruensis*, for example, is remarkable and suggestions from molecular data (Alvarez *et al.* 2007) that it may be due to hybridisation should be further explored.

Genus *Cymbastela* Hooper & Bergquist, 1992

Gender feminine. Type species, by original designation, *Pseudaxinyssa stipitata* Bergquist and Tizard, 1967. Recent, Darwin Harbour, Arafura Sea.

Cymbastela stipitata (Bergquist and Tizard, 1967)
(Figs 7A–B)

Pseudaxinyssa stipitata Bergquist and Tizard, 1967:189; Hooper *et al.* 1992: 265.

Cymbastela stipitata. – Hooper and Bergquist 1992: 106; Hooper and Wiedenmayer 1994 : 75; Alvarez *et al.* 2000: 195; Alvarez and Hooper 2002: 733.

Material examined. Specimens as listed in Hooper and Bergquist (1992). Additional Specimens – Bynoe Harbour, NT: Z.5065 (0M9H2333-C). Darwin Harbour, NT: QM G303262, NTM Z.4078 (0CDN8001-H, Fig. 7A), Z.4104 (0CDN8026-J), Z.4131, Z.4435 (0M9H2008-Y), Z.5064 (0M9H2134-M), Z.5835, Z.5836, Wessel Is, NT: Z.5066 (0M9H2658-H), Z.5067 (0M9H2785-T).

Remarks. *Cymbastella stipitata*, was re-described extensively by Hooper and Bergquist (1992) and the type material re-examined by Alvarez and Hooper (2002). This is one of the most common sponges in the studied area. It is particularly abundant in the intertidal zone of Darwin Harbour, which becomes greatly exposed during the nocturnal king tides of the dry season (May–June) and the diurnal king tides during the wet season (September-November, Fig. 7B). It is found, but less commonly, in subtidal areas down to 19 m depth. New records indicated that its distribution within northern Australia extends from

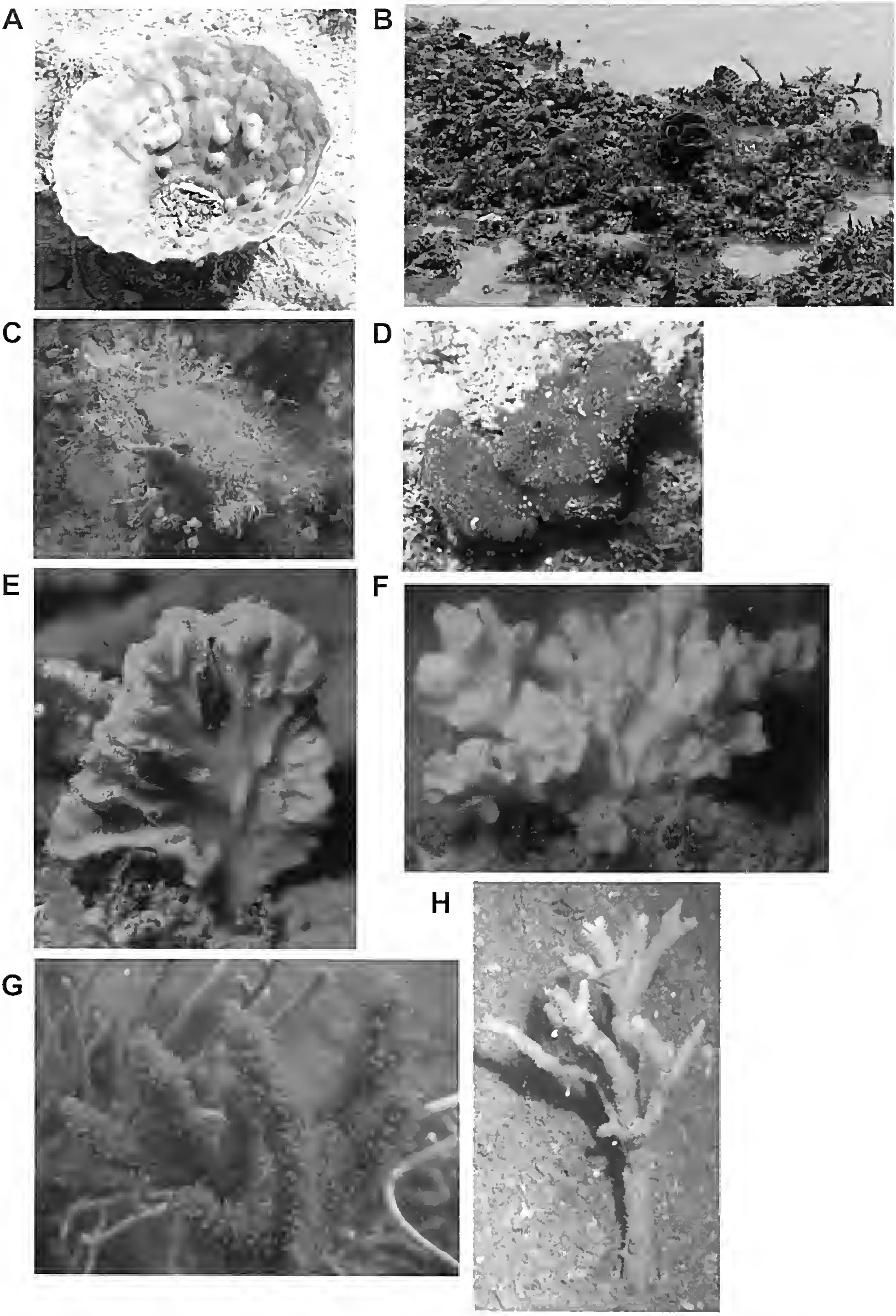

Fig. 7. *Cymbastela stipitata*: **A**, NTM Z.4078 (0CDN-8001-H); **B**, specimens exposed at the reef flat of East Arm, Darwin Harbour during the low tide of 20 September 2001. *Dragmacidon australe*: **C**, specimen at Channel I. Darwin Harbour; **D**, QM G304246, Lizard I, GBR, QLD. *Phakellia tropicalis* sp. nov.; **E**, Holotype (NTM Z.5847); **F**, Paratype (NTM Z.5845). *Reniochalina stalagmites*: **G**, specimen at East Point, Darwin; **H**, specimen at Cotton I., Wessel Is. Photos: **A**, **B**, **E**, **F**, B. Alvarez; **C**, H. Nguyen; **D**, J. Hooper; **G**, A. Ayling; **H**, P. Colin.

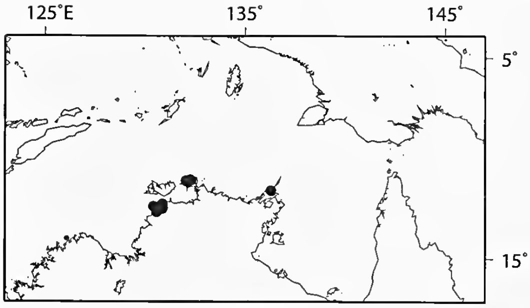

Fig. 8. Distribution of *Cymbastela stipitata*, based on confirmed records from QM and NTM.

Bynoe Harbour to the Wessel Is (Fig. 8), inferring it is a narrow range endemic within northern Australia.

***Cymbastela vespertina* Hooper and Bergquist, 1992**

Cymbastela vespertina Hooper and Bergquist, 1992: 110; Hooper and Wiedenmayer 1994: 75; Alvarez *et al.* 2000: 195; Alvarez and Hooper 2002: 733.

Pseudaxiyssa sp. nov. Hooper *et al.* 1992: 265.

Material examined. Specimens as listed in Hooper and Bergquist (1992).

Remarks. *Cymbastela vespertina* is a sibling species of *C. stipitata*. Separation of the two species based in morphology is difficult and very subjective. Biochemical and molecular evidence (Hooper *et al.* 1992; Alvarez *et al.* 2000) indicates the sympatric populations are heterogeneous. Future genetic population studies might reveal whether or not these populations can be reliably separated into different species, but based on current external gross morphological differences and skeletal characters the two taxa are maintained as distinct.

Remarks on *Cymbastela*. Two species of *Cymbastela* are present within the area of the present study (i.e. *C. stipitata* (Bergquist and Tizard, 1967) and *C. vespertina* Hooper and Bergquist, 1992). Other species of *Cymbastela* represented in other regions including Australia are: *C. cantharella* (Lévi, 1983), New Caledonia; *C. concentrica* (Lendenfeld, 1887), Queensland coast; *C. coralliophila* Hooper and Bergquist, 1992, GBR; *C. marshae* Hooper & Bergquist, 1992, Houman-Abrolhos, WA; *C. notiaina* Hooper and Bergquist, 1992, South Australia; and *C. tricalyciformis* (Bergquist, 1970) from New Zealand. Comprehensive descriptions of these species are given by the respective authors of the species.

Phylogenetic relationships of the genus with other axinellid species based on molecular characters indicate that the northern Australian species of *Cymbastela* are closely related to other members of Dictyonellidae, such as *Acanthella* (Alvarez *et al.* 2000; Erpenbeck *et al.* 2005). There is no doubt, however, that species of *Cymbastela* are related to the Axinellidae based on their morphology. Thus the phylogenetic relationships derived from these molecular analyses remain enigmatic at this stage.

Genus *Dragmacidon* Hallmann, 1917

Gender neuter. Type species, by original designation, *Thrinacophora agariciformis* Dendy, 1905. Recent, Gulf of Manaar, Indian Ocean.

***Dragmacidon australe* (Bergquist, 1970)**

(Figs 7 C–D, 9 A–B)

Pseudaxinella australis Bergquist, 1970: 20; Hooper and Lévi 1993: 1441; Hooper and Wiedenmayer 1994: 80; Alvarez *et al.* 2000: 196.

Dragmacidon australe. – Alvarez and Hooper 2002: 735; Kelly *et al.* 2009 (In press).

Material examined. Holotype – NMNZ Por. 26, Takatu Channel, Northland, New Zealand, 11 m. Additional Specimens – Cartier I, WA: QM G301089. Bynoe Harbour, NT: G303444. Darwin Harbour, NT: NTM Z.5068. Coral Sea, GBR, QLD: QM G300295, G304182, G304246, G304253, G320664, NTM Z.2727.

Description. *Shape* (Fig. 7 C–D). Thickly encrusting, following substrate, globular, bulbous or semispherical, approx. 100 mm in diameter by 20 mm thick.

Colour: Bright red, orange alive.

Consistency. Slightly compressible or stiff. Mucous surface.

Oscula. Irregularly distributed, less than 1 mm diameter, with slightly elevated rims surrounded by thin drainage channels in stellate arrangement.

Surface. Highly conulose; evenly pierced by pores 120–400 µm in diameter. Conules, approx. 1–3 mm long, single or grouped in reticulated pattern, unevenly echinated by spicules, 2–3 mm apart.

Skeleton (Fig. 9A). Plumoreticulate to halichondroid; formed by thick plumose or plumo-echinated multispicular tracts, up to 500 µm thick, ascending nearly perpendicularly from base and becoming thicker and bushy near surface; projecting through ectosome into surface conules. Main tracts connected by shorter and thinner plumose tracts, sometimes ill-defined, forming irregular reticulation of large round meshes.

Spicules (Fig. 9B; Table 4). Oxeas and styles in equal proportions, 176–510 x 7–21 µm (Table 4).

Remarks. The species was originally assigned to *Pseudaxinella* and transferred to *Dragmacidon* by Alvarez

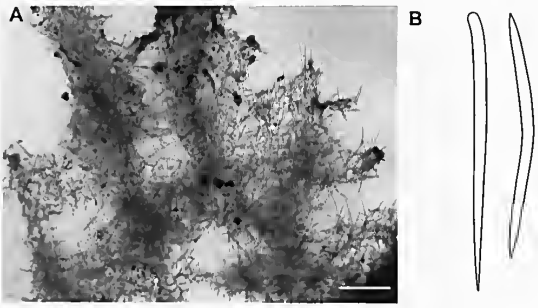

Fig. 9. *Dragmacidon australe*: **A**, light microphotograph of skeleton; **B**, diagram of spicules. Scale bars: **A**, 500 µm; **B**, 50 µm.

Table 4. Comparison of spicule dimensions among specimens of *Dragmacidon australe*. Measurements in micrometres.

Specimen	Locality	Styles	Oxeas
G303444	Bynoe Harbour	254.1–510.4 (349.1±78.8) x 7.3–20.9 (13.6±3)	286.2–434.5 (361.5±39.8) x 7.3–17.9 (13.4±2.4)
Z.5068	Darwin Harbour	176.4–397.3 (290.1±61.4) x 7–17.2 (13±2.8)	271.9–412.5 (340.7±31.9) x 9.5–18.9 (14.3±2.4)

and Hooper (2002) because it conformed more closely with the type species of that genus.

Hooper and Lévi (1993) compared specimens from the GBR with the holotype of *Dragmacidon australe* from New Zealand and with material from New Caledonia described as *D. debitusae* (Hooper and Lévi, 1993). Very subtle differences were found between the two species. The material from northern Australia reported here agrees with *D. australe* in the majority of its features and is therefore assigned to this species. This species is also very similar to *D. reticulatum* (Ridley and Dendy, 1886) from the central West Atlantic both in external morphology and spicule composition.

Distribution. *Dragmacidon australe* was first recorded for New Zealand and additional records from the GBR were reported in Hooper and Lévi (1993). The present revision extends the distribution range of this species into northern Australia. The species is not very common in this region with only isolated records registered through the extension of the studied area (Fig. 10) and thus is probably at the edge of its range. It is also found along more temperate areas of the Queensland coast (Hooper pers. obs.).

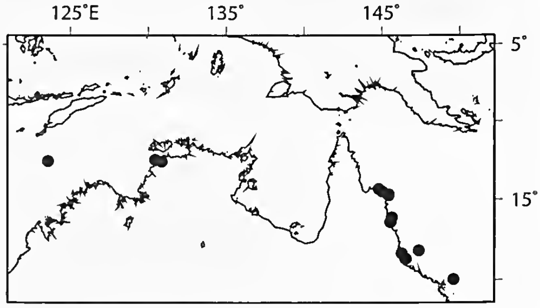

Fig. 10. Distribution of *Dragmacidon australe* in northern Australia, based on confirmed records from QM and NTM. Species distribution extends along the Queensland coast (Hooper pers. obs.) and New Zealand (type locality).

Dragmacidon durissimum (Dendy, 1905)

(Figs 11 A–C)

Thrinacophora durissima Dendy, 1905:187.

Sigmaxinella durissima. – Dendy 1922: 113.

Axinella durissima. – Burton 1959: 259.

Pseudaxinella durissima. – Alvarez *et al.* 2000: 196.

Dragmacidon durissima. – Hallmann 1917: 639; Alvarez and Hooper 2002: 735.

Material examined. Ashmore Reef, WA: QM G300181.

Description. *Shape* (Fig. 11A). Hemispherical, cushion-shaped.

Colour. Orange alive, red on deck, beige in ethanol.

Oscula. Round, irregularly distributed at top, with slightly elevated rims.

Surface. Very rugose, composed of minute projections or conules, compact and close-knit; membranous skin stretched over conules.

Skeleton (Fig. 11B). Plumoreticulate. Multispicular, plumose or plumoechinated spicule tracts, ascending toward surface and connected by shorter and thinner ones, or loose spicules, forming irregular reticulation of oval to square meshes; projecting through ectosome in surface conules or projections.

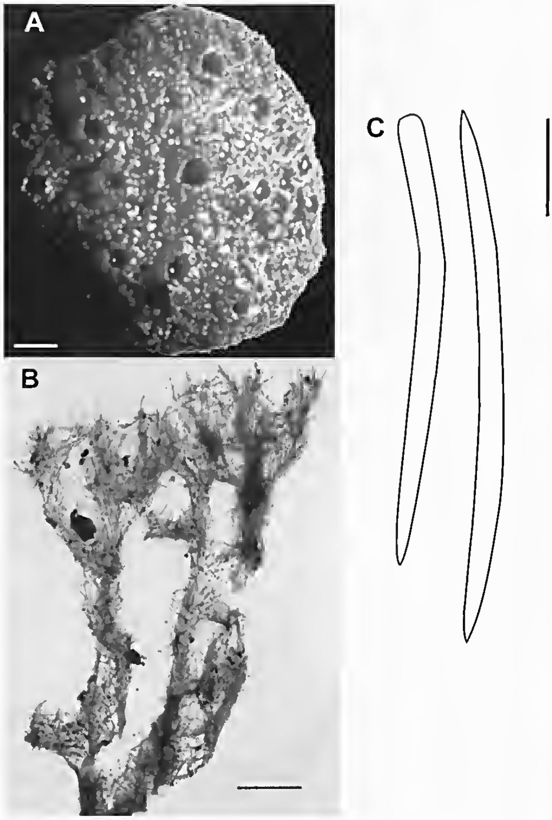

Fig. 11. *Dragmacidon durissimum*: **A**, QM G300181; **B**, light microphotograph of skeleton; **C**, diagram of spicules. Scale bars: **A**, 1 cm; **B**, 500 μm, **C**, 50 μm.

Spicules (Fig. 11C). Styles 203.1–312.5 µm (251.8±33.4) by 11.7–16.4 µm (13.7±1.2). Oxeas in equal proportions, 229.8–312.7 µm (283.2±18) by 7.4–19 µm (13.4±3.1). Trichodragmata short and thick, 15–20 by 5–10 µm.

Distribution. Indian Ocean, including Seychelles Is, Amirante, Providence, Saya de Malha (Dendy 1905; Dendy 1922; Burton 1959), Maldive Is (Alvarez and de Voogd, unpublished data) and Ashmore Reef, Australia.

Remarks. The material examined here agrees in all its characteristics with *Dragmacidon durissimum*, an Indian Ocean species never previously recorded in Australia. Only one specimen from WA was found among the collections examined in this revision. More isolated populations might be present along the WA coast, given that the species is widely distributed throughout the Indian Ocean.

The species was included originally in *Thrinacophora* due the presence of trichodragmata, later transferred to *Sigmaxinella* by Dendy (1922), and subsequently to *Axinella* by Burton (1959) without sufficient justification. Hallman (1917) erected *Dragmacidon* for *D. agariciformis* (Dendy, 1905), *D. durissimum*, *D. clathriformis* (Lendenfeld, 1888) and *D. incrustans* (Whitelegge, 1897). All these species are very similar in habitat, spicule composition and all include trichodragmata. They closely resemble to the West African species *D. lunaecharta* (Ridley and Dendy, 1886). Also similar are the Western Atlantic species *D. reticulatum* (Ridley and Dendy, 1886) and *D. australe* (see above), but they lack trichodragmata.

Remarks on *Dragmacidon*. An additional species of *Dragmacidon* (described as *Pseudaxinella* sp. in Alvarez *et al.* 2000: 196) remains undescribed as no additional material has yet been found to fully characterise the species. The existing material is a fragment of a thin asymmetric lamella, found detached from original substrate that does not agree with the characteristically thickly encrusting shape of *Dragmacidon* species.

Genus *Phakellia* Bowerbank, 1862

Gender feminine. Type species, by original designation, *Spongia ventilabrum* Linnaeus, 1767. Recent, Lervig, Norway, North Sea.

Phakellia tropicalis sp. nov

(Figs 7 E–F, 12 A–B)

Phakellia sp. Alvarez *et al.*, 2000: 195; Holmes and Blanch 2007: 761; Alvarez *et al.* 2007: 1600.

Material examined. Holotype – NTM. Z.5847 (Fig. 7E), Stevens Rock, West Arm, Darwin Harbour, 12°29.1667′S, 130°47.19′E, NT, 9 m depth, 8 May 2006, coll. Alvarez, B. Paratypes – NTM Z.5845 (Fig. 7F), Stevens Rock, West Arm, Darwin Harbour, 12°29.1667′S, 130°47.19′E, NT, 9 m depth, 8 May 2006, coll. B. Alvarez. Additional Specimens – Bynoe Harbour, NT:, NTM Z.4198, Z.4486, Z.4488. Darwin Harbour, NT: NTM Z.866, Z.877, Z.1948, Z.4197, Z.4428, Z.5665, Z.5839–Z.5842, Z.5844, Z.5848, QM G303365, G303383. Wessel Is: NTM Z.4463.

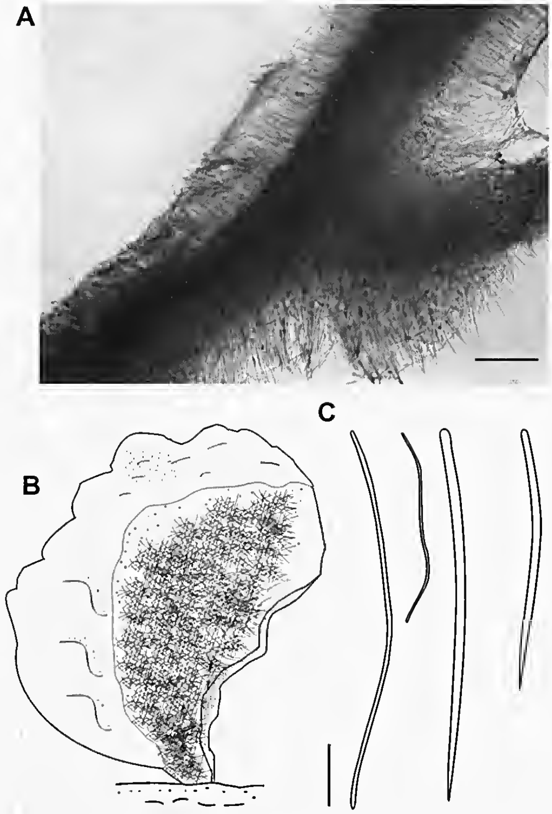

Fig. 12. *Phakellia tropicalis* sp nov.: **A**, light microphotograph of skeleton in cross section; **B**, schematic drawing of skeleton; **C**, diagram of spicules. Scale bars: **A**, 500 µm; **B**, 100 µm.

Papua New Guinea: QM G312926, G312937. Malaysia: NTM Z.5843.

Description. *Shape* (Fig. 7E–F). Small convoluted thin fans, up to 250 mm high and 300 mm wide, on short and thin peduncle, flexible, less than 5 mm thick, arranged in multiple planes, with fluted or planar flanges, ragged or crenulated margins.

Colour. Bright orange, beige-orange, or yellow-brown (Darwin and Bynoe Harbour specimens) alive.

Oscula. Star-shape oscula, minute.

Surface. Velvety, felty, with choanosomal spicules projecting shortly; marked with fine network of excurrent channels ending in oscula and reinforced close to the peduncle by thick choanosomal axes or 'veins'.

Skeleton (Fig. 12A, B). A core of interwoven spicules, occupying most of specimen's thickness, laterally compressed, echinated by a dense palisade of single spicules, sometimes aggregated in loose brushes, protruding through surface.

Spicules (Fig. 12C). Strongyles wavy, 222–800 in length by 3–8 µm thick and styles 231–703 in length by 6–16 µm thick (Table 5).

Remarks. (see Carvalho *et al.* 2007 for extensive review of *Phakellia* species.)

The species is atypical of *Phakellia*, although it agrees with the diagnosis given by Alvarez and Hooper (2002) in most aspects. It is fan-shaped, with styles projecting through the ectosome, and includes the typical spicule composition of the genus. However the reticulation of thick 'veins' or thick axes observed in most species of *Phakellia*, seems to be either incomplete or obscured by the habit of the species here described.

The skeleton of this species (especially when seen in cross section, as in Fig. 12A) resembles some species of *Acanthella* (Dictyonellidae), a genus often confused with *Phakellia*. *Phakellia tropicalis* however, lacks two of the main diagnostic features of *Acanthella* – the cartilaginous to membranous surface and the cavernous structure of the choanosomal skeleton, with sheets of aspiculous collagen joining the primary axes in the skeleton. Instead, the surface of *P. tropicalis* is velvety, felty, with choanosomal spicules projecting shortly through the surface, a character shared with other axinellid genera such as *Axinella* and *Cymbastela*, and the skeleton is formed by a core of interwoven strongyles with a regular and dense palisade of erect styles that occupies most of the thickness of the sponge.

A phylogenetic analyses based on morphological characters by Alvarez *et al.* (2000) showed this species to be closely related to other species of *Acanthella* (i.e. *A acuta*, *A. cavernosa* and *A. pulcherrima*). In the same study, however, an analysis based on 28S rDNA sequences with the same set of species, indicated that *P. tropicalis* was closely related to typical axinellid genera such as *Axinella* and *Dragmacidon* supporting its allocation to Axinellidae instead of Dictyonellidae.

Furthermore, the skeletal architecture of *P. tropicalis* corresponds with the basic plan observed in species of *Bubaris* Gray, 1867, a genus of the family Bubaridae and currently used in the strict sense to include encrusting forms (Alvarez and Van Soest 2002). Thus, one could interpret the new species as an 'erect *Bubaris*' and be tempted to allocate it to that genus. It is possible that species with erect forms originally described under *Bubaris*, but transferred to *Acanthella* and *Phakellia* in order to preserve the revised concept of Bubaridae by Alvarez and Van Soest (2002), might be related to the new species. If that is the case, those species could be grouped under a new genus following a revised version of Hentschel's (1923) concept of Bubaridae, which accepted sponges of erect forms, where the core of interwoven strongyles echinated by styles is placed in the centre (or in the axis) instead of at the base, as in the encrusting forms. However, it would be premature to erect a new genus here based on the characteristic of one single species and without re-examining species currently hidden under *Acanthella* or *Phakellia* which might also share such characteristics and could justify the creation of the new genus. In the absence of such evidence, we assign the new species provisionally to *Phakellia* and propose to expand the definition of Alvarez and Hooper (2002) (and modified by Carvalho *et al.* 2007) as: Axinellidae of planar habit, with skeleton formed by multiple axes or a single core of sinuous megascleres (frequently strongyles), echinated either by single spicules or by secondary tracts of a second class of megascleres (frequently styles).

Phakellia tropicalis is the only species of *Phakellia* recorded in this study and as far as we know the first one recorded from warm waters and shallow depths. Note that some species currently accepted under *Phakellia* from similar habitats are likely to be misidentifications (see Carvalho *et al.* 2007 for an extensive review of *Phakellia* species). Other species of *Phakellia* recorded from northern Australia and adjacent areas are currently accepted under *Acanthella* (Van Soest *et al.* 2008) or *Axinella* (i.e. *Phakellia aruensis* Hentschel, 1912, see above). Yet other species described under *Phakellia* in the Indian Ocean are not typical of the genus: *P. ceylonensis* Dendy, 1905: 192 is an *Axinella* (see above); *P. crassistylifera* Dendy, 1905: 192 is likely to belong in *Stylissa* and *Phakellia ridleyi* Dendy, 1887: 159 is currently accepted as a species of *Phakettia*.

Distribution. This species is found along the NT coast and is very common in both Darwin and Bynoe harbours. It is also recorded for Papua New Guinea and Malaysia. It is found between 5–20 m depth

Etymology. Referring to its tropical habitat. It is intended as a noun in apposition.

Genus *Reniochalina* Lendenfeld, 1888

Gender feminine. Type species, by subsequent designation of Hallmann (1914), *Reniochalina stalagmitis* Lendenfeld, 1888. Recent, Western Australia.

Reniochalina stalagmitis Lendenfeld, 1888

(Figs 7G–H, 13A–F, 14 A–E, 15)

Reniochalina stalagmitis Lendenfeld, 1888: 82; Whitelegge 1902: 283; Hallmann 1914: 346; Hooper and Wiedenmayer 1994: 81; Hooper and Lévi 1993: 1404; Alvarez, *et al.* 2000: 197; Alvarez and Hooper 2002: 746; Holmes and Blanch 2007.

Axinella echidnaea. – Ridley 1884: 462; Kieschnick 1896: 533; Hentschel 1912: 419 [misidentification; not Ridley and Dendy 1887: 183]

Reniochalina lamella Lendenfeld, 1888: 83; Whitelegge 1902: 283; Hallmann 1914: 346.

Axiamon folium Hallmann, 1914: 441 [objective synonym, see Wiedenmayer (1989: 49) and Hooper and Lévi (1993: 1403)]

Material examined. Type material – *Reniochalina stalagmitis*: Lectotype, BMNH 1887.4.27.122, Western Australia, Fig. 13A; paralectotype, AM G9004, wet, West Australia, Fig. 13B [also holotype of *Axiamon folium*]. *Reniochalina lamella*: AM B5478, syntype, wet, no locality data [also paratype of *A. folium*]. Additional specimens – Ridley's (1884) material: BMNH 1882.2.23.261, Prince of Wales Channel, Torres strait, North Queensland, coll. HMS *Alert*; BMNH 1881.10.21.259, Thursday I., Torres strait, North Queensland, coll. HMS *Alert*. Hentschel's

Table 5. Comparison of spicule dimensions among specimens of *Phakellia tropicalis*. Measurements in micrometres.

Specimen	Locality	Strongyles	Styles
Z.5847	Holotype, Stevens Rock	284.1–651.2 (480.4±105.3) x 3.8–8.4 (5.7±1.2)	231.9–549.2 (385.7±82.5) x 7.3–430.9 (29.8±83.6)
Z.4488	Bynoe Harbour	222.8–670.7 (435.5±135) x 3.7–9.5 (7±1.6)	353.9–703.6 (484.6±102.2) x 9–16.4 (13.8±2)
Z.4463	Wessel Is	293.1–800 (553.4±134.6) x 4.4–8.4 (6.6±1.1)	273.6–658.2 (439.6±111.1) x 8.3–16 (11.2±2.2)
G312926	Papua New Guinea	277.8–696.3 (476.4±117.6) [24] x 4.2–8.4 (6.3±1.1)	239.6–490.6 (343.5±69.5) x 5.9–11.5 (8.7±1.8)

(1912) specimen, SMF 1687, Aru-Inseln, bei Pulu Bambu, Indonesia, 10 m depth, 3 April 1908, coll. H. Merton, dredge. NW Shelf, WA: NTM Z.2358, Z.2361, Z.2273, Z.724, Z.738. Ashmore reef, WA: QM G301093, G301112, G301139. NE Joseph Bonaparte Gulf, QM G301202. Fog Bay, NT, QM G303548. Bynoe Harbour, NT: NTM, Z.4462 (0M9H2388-N), Z.5074 (0M9H2451-H), Z.5853. Darwin Harbour, NT: QM G303329, G303362, G303374, G303579, NTM Z.227, Z.285, Z.474, Z.483, Z.815, Z.1107, Z.1989, Z.2686, Z.4448 (0M9H2005-V), Z.5854, Z.5855, Gunn Point, NT, QM G303535. Parry Shoals, NT, Z.525. Melville I., NT, NTM Z.608. Cobourg Peninsula, NT: NTM Z.67, Z.135, Z.537, Z.565, Z.1335, Z.2527. Groote Eylandt, NT, G313555. Wessel Is, Z.5075 (0M9H2647-T). Gulf of Carpentcria, NT, QM G300817. Torres Strait, QM G316882.

Description. *Shape* (Figs 7G–H, 13 A–B). Arborescent, branching or fan-shaped, generally stalked, and erect with specimens up to 60 cm high. Branches, flat to cylindrical, dichotomous or fused, 1–2 cm diameter, generally with pointed tips, dividing and anastomosing irregularly in different planes.

Colour. Two colour forms, orange-red and beige-yellow. Always brown in alcohol.

Oscula. Small, less than 5 mm diameter, with elevated rims thin, membranous and transparent, irregularly distributed through the branches.

Surface. Long surface processes or conules with projecting spicules, up to 5 mm long, evenly distributed and separated by more-or less longitudinal and parallel channels, 1 mm apart, 1 mm deep.

Skeleton (Fig. 13C–F). Specialised ectosomal skeleton absent; choanosomal skeleton differentiated into axial and extra-axial regions. Extra-axial skeleton reticulated with ascending spongin fibres, 50–100 µm interconnected at all angles by single spicules or short fibres, or anastomosing and forming oval to round meshes up to 200 µm in diameter; spongin fibres slightly developed and cored with paucispicular tracts of spicules, sometimes plumose; projecting into surface processes and becoming dense and disorganised at tips. Axial skeleton slightly condensed and reticulated as in extra-axial region.

Spicules (Fig. 14A–E; Table 6). Oxeas or anisoxeas, occasionally modified to styles, straight, bent or slightly sinuous; with tips surmounted by microspines, which might be rudimentary or absent; microspines at one end might be half the compared size to those at other end (175–450 x 6–20 µm). Thin, sinuous styles or oxeas with smooth or slightly spined ends, 156–288 x 3–6 µm (Fig. 14A–C), scattered through the choanosomal skeleton, rare in most examined specimens. Few long styles, projecting through ectosome, present in some specimens but extremely rare.

Remarks. The thin and sinuous styles (Fig. 14) were first mentioned by Hallmann (1914) in his description of *Axiamon folium*. The presence of these spicules was confirmed in all the specimens examined here and point out relationships of *Reniochalina* with other members of the family Raspailiidae (order Poecilosclerida). Long and slightly sinuous styles, most of which were broken, were also observed in the type material of *Axiamon folium* (AM G9004) and in some of the specimens examined. These were extremely rare and scattered throughout the extra-axial skeleton and projecting through the surface, indicating further affinities with raspailid taxa and challenging the position of the genus within Axinellidae (see below).

Distribution. *Reniochalina stalagmitis* is one of the most abundant sponge species of northern Australia. It is found from the intertidal to depths of 60 m. Its distribution extends well beyond the boundaries of the studied region (Fig. 15) with validated records from the northern region of WA (down to W Buccaneer Archipelago) and QLD (down to the Howick Is region). It also occurs in Indonesia.

Notes on *Reniochalina*. *Reniochalina* was defined by Alvarez and Hooper (2002) as 'Axinellidae with extra-axial spongin fibres projecting into surface processes and cored with paucispicular tracts of oxeas, anisoxeas and styles. Oxeas with tips surmounted by micro-spines'.

The genus was considered to be closely related to other axinellid genera (i.e. *Ptilocaulis* and *Phycopsis*) by Alvarez and Hooper (2002), based on the shared presence of conspicuous, long, filamentous surface processes and their skeletal features. The close affinities with *Ptilocaulis* were further confirmed by molecular phylogenetic analyses (Alvarez *et al.* 2000). Recent molecular studies (Erpenbeck *et al.* 2007; Holmes and Blanch 2007) also showed strong affinities of *Reniochalina stalagmitis* with the raspaillid species *Axechina raspailoides*. As previously indicated (Hooper 1991; Hooper 2002b), these species have similar growth forms and choanosomal skeletons, and it is now confirmed that they also share the presence of styles

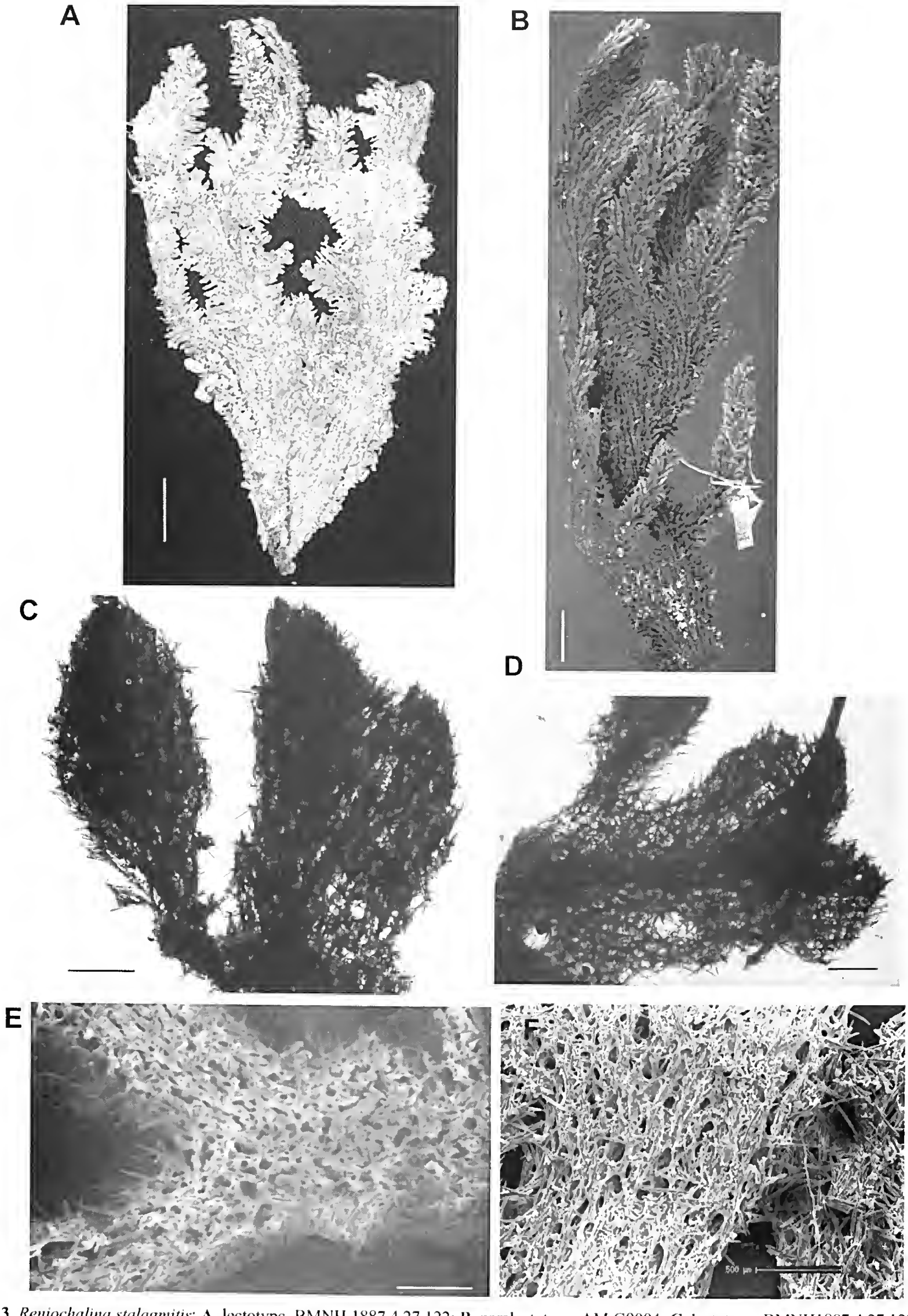

Fig. 13. *Reniochalina stalagmitis*: **A**, lectotype, BMNH 1887.4.27.122; **B**, paralectotype, AM G9004; **C**, lectotype, BMNH1887.4.27.122, light microphotograph of skeleton; and **D**, SEM of skeleton; **E**, paralectotype, AM G9004, light microphotograph of skeleton and **F**, SEM of skeleton. Scale bars: **A**, **B**, 2 cm; **C–F**, 500 µm.

with spined tips and identical shape (Fig. 14B, C), a fact overlooked by previous authors with the exception of Hallmann (1914).

Additional molecular analysis based on the CO1 fragment (Erpenbeck 2007) also indicated affinities of the Caribbean species *Ptilocaulis marquezi* (Duchassaing and Michelotti, 1864) with other raspailiid species (i.e. *Pandaros acanthifolium* (Duchassaing and Michelotti, 1864) and *Ecyoplasia ferox* (Duchassaing and Michelotti, 1864) suggesting strongly that both *Ptilocaulis* and *Reniochalina* are closely related to the Raspailiidae. These relationships however, remain unresolved as neither *Reniochalina* nor *Ptilocaulis* have the typical raspailiid ectosomal skeleton which is clearly present in *Axechina* and other raspailiid taxa. Unfortunately, the range of taxa sampled in the molecular analyses mentioned above was inadequate to conclude further on the affinities of the axinellid genera *Reniochalina* and *Ptilocaulis* (and likely *Phycopsis* too) with the family Raspailiidae. Therefore, if more evidence from molecular analyses becomes available to support the current results, these genera might be relocated to the Raspailiidae.

Other species of *Reniochalina* reported in the literature do not agree with the current definition of the genus and are referred here to more appropriate genera: *Reniochalina condylia* Hooper and Lévi, 1993, to *Dragmacidon*; *R. plumosa* Lévi and Lévi, 1983 to *Axinella* and, *R. sectilis* Wiedenmayer, 1989 to *Rhaphoxya* in Dictyonellidae. Additional species of *Reniochalina* including *Reniochalina* sp., reported in Alvarez *et al*. (2000), remain to be described from other areas of Australia (Hooper, pers. obs.). It is likely also that some species of *Reniochalina* are misidentified as species of *Ptilocaulis* (e.g. *P. rigidus* Carter, 1883:322).

DISCUSSION

The results of this revision indicate that the Axinellidae is represented in the area covered by this study by only five genera (i.e. *Axinella, Cymbastela, Dragmacidon, Phakellia* and *Reniochalina*) and nine species, three of which are new. Data gathered from NTM and QM collections during the initial stages of this revision indicated that the Axinellidae was represented in the area by a larger number of species. This observation turned out to be contrary to what was found after a thorough examination of recorded material. Many of the species thought to belong to the Axinellidae were in fact found to be members of other families and orders, particularly Raspailiidae (Poecilosclerida).This reflects that separation of species within this group is extremely subjective and could be erroneous if is taken in an isolated context. Examination of the taxonomic characters across a large number of specimens is critical to detect the variability and plasticity of morphological characters present in this group and to avoid incorrect splitting of taxa. It is possible that cryptic species or hybrid forms are hidden within the continuum of variability commonly observed in species of Axinellidae; but only results of population genetic studies can reveal such cryptic species, and indeed verify the occurrence of hybridisation among the Porifera, as has been demonstrated for the Cnidaria (e.g. Veron 1995, Van Oppen 2000 and references within).

The five remaining genera of the Axinellidae (i.e. *Auletta, Dragmaxia, Pipestela, Ptilocaulis* and *Phycopsis*) are curiously not represented in the studied material despite the fact that they do include tropical species.

Axinella loribellae, *Cymbastela stipitata* and *C. vespertina* are the only species of axinellids reported here with distributions restricted to northern Australia, reflecting some degree of endemism in the area. The latter sibling species pair represent western components of east-west coast species pairs of the genus *Cymbastela*, with *C. coralliophila* and *C. concentrica* of the east coast, presumed remnants of Pleistocene separation of northern Australian faunas during low strand sea levels (e.g. Hooper and Ekins 2004). *Axinella sinoxea* displays a similar distribution but can be found in deep waters of WA. The remaining species seem to have a more widespread distribution throughout Indonesia, Papua New Guinea and Malaysia. *Axinella aruensis* and *Reniochalina stalagmitis* are widely distributed in the northern region of Australia and Indonesia. *Dragmacidon australe* has a disjunct distribution with isolated records from New Zealand, GBR and northern

Table 6. Comparison of spicule dimensions among specimens of *Reniochalina stalagmitis*. Measurements in micrometres.

Specimen	Locality	Oxeas	Thin styles/oxeas
Lectotype BMNH1887.4.27.122	WA	190–315 (248.6±27.9) x 8–15.2 (12.1±2.4)	157.1–287.6 (240.2±35.3) [18] x 2.6–5.8 (4.5±0.9) [18]
AM G9004	WA	175–450 (243.9±61.8) x 7.9–20 (10.7±3)	211.7–268 (244±22.7) [9] x 2.6–5 (3.8±0.8) [9]
AM B5478	WA	197–376.6 (248.3±49.5) x 10.1–19 (14.4±1.9)	156.4–235 (203.7±25.3) [12] x 3.5–6.3 (4.9±0.8) [12]
G303362	Darwin	209.1–356.6 (253.3±43.4) x 9.2–17 (13±2.2)	206.5–232.6 (219.5±18.4) [2] x 3.9–4 (3.9±0) [2]
Z.4462	Bynoe Harbour	195.1–379.1 (293.5±39.1) x 7.1–18.2 (13.9±2.6)	158.2–244.4 (213.2±40.2) [4] x 2.6–5.2 (4.2±1.1) [4]
Z.5075	Wessel Is	199.6–380.2 (286.4±44.6) x 6.3–18 (12.4±2.8)	205.8x3.7 [1]

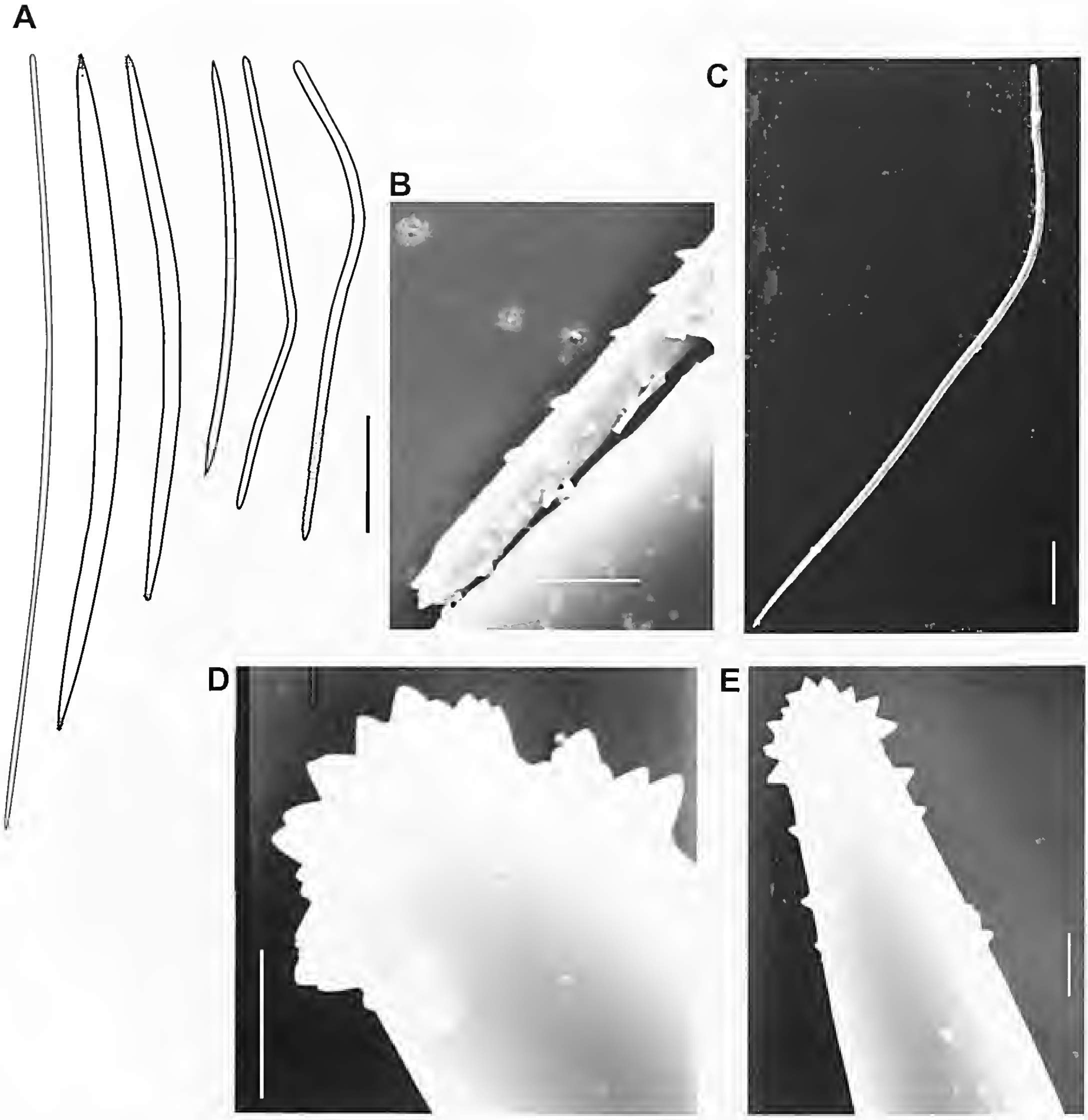

Fig. 14. *Reniochalina stalagmitis*: A, diagram of spicules; B, C, SEM of sinuous style with spined tip (AM G9004); D, E, tip of oxeas, (AM G9004). Scale bars: A, 50 µm; B, 5 µm; C, 20 µm; D, E, 2 µm.

Australia. *Dramacidon durissimum* is a species common from Indian Ocean but its distribution is now extended to the Ashmore Reef, WA of northern Australia.

The position of *Reniochalina* within the Axinellidae is now debatable. The presence of sinuous styles with spiny tips in *R. stalagmitis* and the recent evidence based on molecular data (see above) suggest strongly that the species is closely related to the raspailiid species *Axechina raspailioides* (Poecilosclerida) and challenges the position of *Reniochalina stalagmitis* within the family. The typical ectosomal skeleton present in raspailiid species and considered a synapomorphy for that family is absent in *R. stalagmitis*, thus no definitive conclusions can be made at this stage. New studies as suggested above are needed

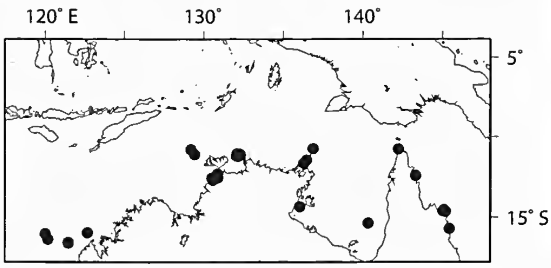

Fig. 15. Distribution of *Reniochalina stalagmitis* in northern Australia, based on confirmed records from QM and NTM. Species distribution extends along the Queensland coast (Hooper, unpublished data).

to decide whether *Reniochalina* should remain classified under the Axinellidae.

Phylogenetic relationships within the family Axinellidae and other related groups have been explored previously, using either morphological, molecular or chemical characters (Alvarez *et al.* 2000; Erpenbeck *et al.* 2002; Erpenbeck *et al.* 2005; Erpenbeck *et al.* 2006; Erpenbeck *et al.* 2007). The relationships shown in those studies remain inconclusive at this stage but suggest strongly that the Axinellidae is a polyphyletic taxon with uncertain affinities. The taxonomic revision of species of the Axinellidae and its sister groups is critical to support conclusions derived from those studies and is currently the focus of ongoing studies undertaken at regional basis (e.g. Indonesia, Eastern Australia, Central-West Pacific, Southern Australia and New Zealand).

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APPENDIX

Collection and locality data of material examined in the collections of QM and NTM.

QM material

G300181	Passage West I., outer reef, Ashmore Reef, WA, 12°14′S, 122°56′E, 15.5 m, 27 Jul 1986, coll. Hooper, JNA
G300295	Snake Reef, Howick Group, GBR, QLD, 14°27′S, 145°1′E, 12.5 m, 14 Dec 1990, coll. Hooper, JNA
G300609	N side of Cumberland Strait, Wessel Is, Gove, NT, 11°28′S, 136°29′E, 13 m, 14 Nov 1990, coll. NCI, AIMS
G300759	Marinbar I, SE Cape Wessel, Wessel Is, NT, 11°1.13′S, 136°46.04′E, 20 m, 17 Nov 1990, coll. NCI, AIMS
G300768	Gugari Rip 100m NE, E Guluwuru I, Wessel Is, NT, 11°34′S, 136°22.12′E, 8 m, 13 Nov 1990, coll. NCI, AIMS
G300817	Duyfken Point, W Gulf of Carpentaria, QLD, 12°34′S, 141°0′E, 58 m, 26 Nov 1991, coll. Cook, SD. on CSIRO RV Southern Surveyor
G301089	Cartier I, outer reef slope, N side reef, WA, 12°31.07′S, 123°33.05′E, 14 m, 6 May 1992, coll. Hooper, JNA
G301092	Cartier I, outer reef slope, N side reef, WA, 12°31.07′S, 123°33.05′E, 22 m, 7 May 1992, coll. Hooper, JNA
G301093	Cartier I, outer reef slope, N side reef, WA, 12°31.07′S, 123°33.05′E, 22 m, 7 May 1992, coll. Hooper, JNA
G301112	Cartier I, outer reef slope, S side of reef, WA, 12°32.15′S, 123°33.12′E, 23 m, 8 May 1992, coll. Hooper, JNA
G301139	Hibernia Reef, entrance to lagoon, NE side reef, WA, 11°57.13′S, 123°22.06′E, 23 m, 10 May 1992, coll. Hooper, JNA
G301197	Flattop Bank, NE Joseph Bonaparte Gulf, NT, 12°16′S, 129°15′E, 32 m, 17 May 1992, coll. Hooper, JNA
G301202	Flattop Bank, NE Joseph Bonaparte Gulf, NT, 12°16′S, 129°15′E, 32 m, 17 May 1992, coll. Hooper, JNA
G303262	South Shell I., reef N of boat ramp, East Arm, Darwin Harbour, NT, 12°29.1334′S, 130°53.09′E, 0 m, 19 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303322	East Point Bommies, Darwin Harbour, NT, 12°24.08′S, 130°48.14′E, 10 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303329	East Point Bommies, Darwin Harbour, NT, 12°24.08′S, 130°48.14′E, 10 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303332	East Point Bommies, Darwin Harbour, NT, 12°24.0834′S, 130°48.14′E, 10 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303362	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303365	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303374	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 19 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303383	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303388	Stevens Rock, West Arm, Darwin Harbour, 12°29.1667′S, 130°47.19′E, NT, 19 m depth, 24 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303444	Fish Reef, west side, Bynoe Harbour, NT, 12°26.01′S, 130°26.09′E, 11 m, 26 Sep 1993, coll. Hooper, JNA and Hobbs, LJ
G303535	Shoal Bay, W Gunn Point, NT, 12°9.15′S, 130°56.02′E, 14 m, 11 Oct 1993
G303548	Fog Bay, 1 nml E Point Blaze, NT, 12°54.15′S, 130°7.16′E, 7 m, 4 Oct 1993
G303579	Lee Point near Anglers Reef, Darwin Harbour, NT, 12°18.13′S, 130°52.14′E, 10 m, 11 Oct 1993
G304182	Granite Bluff, Lizard I., S headland Mermaid Cove, QLD, 14°39′S, 145°27′E, 18 m, 4 Apr 1994, coll. Hooper, JNA and party
G304246	Cobia Hole, Mrs Watson's Bay, Lizard I., QLD, 14°39.03′S, 145°26.15′E, 18 m, 5 Apr 1994, coll. Hooper, JNA and party
G304253	Palfrey I., W side, Lizard I., QLD, 14°42.03′S, 145°26.09′E, 16 m, 6 Apr 1994, coll. Hooper, JNA and party
G310136	Parry Shoals 35nm W Bathurst I., NT, 11°7.03′S, 129°25.9′E, 16 m, 12 Aug 1987
G311873	100m NE Gugari Rip, East side Guluwuru IS, Wessel Is, NT, 11°20.4′S, 136°13.63′E, 8 m, 13 Nov 1990
G312926	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.05′S, 148°10.14′E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312913	Coutance Islet, Kupiano, SE. Papuan Barrier Reef, Papua New Guinea, 10°14.0167′S, 148°6.14′E, 41 m, 14 Dec 1996, coll. Hooper, JNA
G312935	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501′S, 148°10.14′E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312937	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.05′S, 148°10.14′E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G313555	S Groote Eylandt, NT, 14°27.1801′S, 136°14.29′E, 22.5 m, 12 Oct 1997, coll. Cook, SD. on CSIRO RV Southern Surveyor
G316882	Torres Strait, QLD, 10°46.8′S, 142°15′E, 16.4 m, 19 Jan 2004, coll. TSMap_GM_01_2004 Gwendoline May
G320664	Munro Reef, Coral Sea, QLD, 14°18.15′S, 144°48.82′E, 23 m, 2 Jul 2003, coll. Hooper, JNA and party

APPENDIX (continued)

Collection and locality data of material examined in the collections of QM and NTM.

NTM material

Z.67	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.50'S, 132°3.01'E, 17 Oct 1981, coll. Hooper, JNA & Alderslade, PN
Z.135	Sandy I. No.2, Cobourg Peninsula, NT, 11°5.50'S, 132°17'E, 10 m, 21 Oct 1981, coll. Hooper, JNA & Alderslade, PN
Z.227	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 14 Nov 1981, coll. Hooper, JNA
Z.285	Dudley Point Reef, East Point, Darwin, NT, 12°25.00'S, 130°48.01'E, 1 m, 18 Sep 1981, coll. Hooper, JNA & Murray, P
Z.474	Fannie Bay, Darwin, NT, 12°25.00'S, 130°50'E, 9 Feb 1982, coll. Hooper, JNA
Z.483	Fannie Bay, Darwin, NT, 12°25.00'S, 130°50'E, 9 Feb 1982, coll. Hooper, JNA
Z.525	Parry Shoals 35nm W Bathurst I., NT, 11°7.03'S, 129°25.9'E, 1 m, 30 Apr 1982, coll. Hooper, JNA & Alderslade, PN
Z.537	Port Bremer, Cobourg Peninsula, NT, 11°8.5'S, 132°18.8'E, 1 May 1982, coll. Hooper, JNA & Alderslade, PN
Z.565	Sandy I. No.2, Cobourg Peninsula, NT, 11°5'S, 132°16.51'E, 14 m, 2 May 1982, coll. Hooper, JNA
Z.608	Cootamundra Shoals, North of Melville I., NT, 10°49.07'S, 129°12.09'E, 31 m, 6 May 1982, coll. Thom, B & Lockyer, R
Z.615	Cootamundra Shoals,North of Melville I., NT, 10°50.22'S, 129°13.17'E, 22 m, 10 May 1982, coll. Lockyer, R
Z.619	Unnamed shoal N Melville I, NT, 11°38.23'S, 129°51.00'E, 24 m, 17 May 1982, coll. Thom, B & Lockyer, R
Z.630	Unnamed shoal N Melville I, NT, 11°32.58'S, 130°02.50'E, 18 m, 25 May 1982, coll. Lockyer, R
Z.631	Unnamed shoal N Melville I, NT, 11°32.58'S, 130°02.50'E, 18 m, 25 May 1982, coll. Lockyer, R
Z.632	Unnamed shoal N Melville I, NT, 11°32.57'S, 130°2.51'E, 18 m, 25 May 1982, coll. Lockyer, R
Z.665	NW Yampi Sound, NW Shelf, WA, 15°27.0334'S, 121°49.01'E, 76 m, 29 Apr 1982, coll. CSIRO R.V. Sprightly
Z.724	N Adele I.,Collier Bay, NW Shelf, WA, 15°58.02'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V. Sprightly
Z.738	N Adele I.,Collier Bay, NW Shelf, WA, 15°58.02'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V. Sprightly
Z.815	Channel I., Middle Arm, Darwin, NT, 12°32.02'S, 130°51.02'E, 11 m, 16 Jul 1982, coll. Scott Chidgey (Caldwell Connell Ass
Z.822	Channel I., Middle Arm, Darwin, NT, 12°33.08'S, 130°51.04'E, 20 m, 18 Jul 1982, coll. Scott Chidgey (Caldwell Connell Ass)
Z.866	Channel I., Middle Arm, Darwin, NT, 12°32.07'S, 130°52.04'E, 13 m, 20 Aug 1982, coll. Alderslade, PN.
Z.868	Channel I., Middle Arm, Darwin, NT, 12°32.07'S, 130°52.04'E, 13 m, 20 Aug 1982, coll. Alderslade, PN.
Z.877	Channel I., Middle Arm, Darwin, NT, 12°32.07'S, 130°52.04'E, 13 m, 20 Aug 1982, coll. Alderslade, PN.
Z.1107	Dudley Point Reef, East Point, Darwin, NT, 12°25.00'S, 130°48.01'E, 22 Dec 1982, coll. Hooper, JNA
Z.1335	Table Head, Port Essington, Cobourg Peninsula, NT, 11°13.5'S, 132°10.51'E, 11 May 1983, coll. Hooper, JNA
Z.1363	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S, 132°3.71'E, .5–6 m, 16 May 1983, coll. Hooper, JNA
Z.1388	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S, 132°3.71'E, 6 m, 17 May 1983, coll. Hooper, JNA
Z.1948	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.2'S, 130°47.1'E, 27 Apr 1984, coll. Hooper, JNA
Z.1961	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.2'S, 130°47.1'E, 27 Apr 1984, coll. Hooper, JNA
Z.1989	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, m, 11 May 1984, coll. Hooper, JNA and party
Z.2156	Northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2'S, 130°37.61'E, 5 Oct 1984, coll. Hooper, JNA
Z.2246	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 m, 12 Apr 1985, coll. Hood, C and party
Z.2249	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 m, 12 Apr 1985, coll. Hood, C and party
Z.2273	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2284	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2304	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2310	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2322	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2331	NW Lacepede Is, NW Shelf, WA, 16°31.00'S, 121°28.01'E, 38–40 m, 17 Apr 1985, coll. Russell, BC (TRASH Fish project)
Z.2345	NW Lacepede Is, NW Shelf, WA, 16°34'S, 121°27.01'E, 40–46 m, 17 Apr 1985, coll. Russell, BC
Z.2358	NW Lacepede Is, NW Shelf, WA, 16°34'S, 121°27.01'E, 40–46 m, 17 Apr 1985, coll. Russell, BC
Z.2361	NW Lacepede Is, NW Shelf, WA, 16°34'S, 121°27.01'E, 40–46 m, 17 Apr 1985, coll. Russell, BC
Z.2402	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 8 m, 29 Jul 1985, coll. Hooper, JNA
Z.2511	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S, 132°3.71'E, 15 Sep 1985, coll. Hooper, JNA

APPENDIX (continued)

Collection and locality data of material cxamined in the collections of QM and NTM.

NTM material

Z.2526	Orontes Reef,mouth of Port Essington,Cobourg Peninsula, NT, 11°3.60'S, 132°5.41'E, 18–20 m, 16 Sep 1985, coll. Hooper, JNA
Z.2527	Orontes Reef,mouth of Port Essington,Cobourg Peninsula, NT, 11°3.60'S, 132°5.41'E, 18–20 m, 16 Sep 1985, coll. Hooper, JNA
Z.2529	Orontes Reef,mouth of Port Essington,Cobourg Peninsula, NT, 11°3.60'S, 132°5.41'E, 17 Sep 1985, coll. Hooper, JNA
Z.2632	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2686	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2719	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2727	Myrmidon Reef,GBR, QLD, 18°10.00'S, 147°23'E, 15 m, 1 Jan 1985, coll. Wilkinson,CR
Z.3062	Parry Shoals, Arafura Sea, NT, 11°11.72'S, 129°43.26'E, 16 m, 12 Aug 1987, coll. Mussig, AM and NCI team
Z.3068	Parry Shoals, Arafura Sea, NT, 11°11.72'S, 129°43.26'E, 16 m, 12 Aug 1987, coll. Mussig, AM and NCI team
Z.3137	Parry Shoals, Arafura Sea, NT, 11°12.27'S, 129°42.71'E, 16 m, 14 Aug 1987, coll. Mussig, AM and NCI team
Z.3141	Parry Shoals, Arafura Sea, NT, 11°12'S, 129°43.01'E, 16 m, 14 Aug 1987, coll. Mussig, A.M. and NCI (AIMS)
Z.3922	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3925	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3935	N side of Cumberland Strait, Wessel Is, Gove Peninsula, NT, 11°27.60'S, 136°28.7'E, 32 m, 15 Nov 1990, coll. Hooper, JNA
Z.3936	N side of Cumberland Strait, Wessel Is, Gove Peninsula, NT, 11°27.60'S, 136°28.7'E, 32 m, 15 Nov 1990, coll. Hooper, JNA
Z.3938	N side of Cumberland Strait, Wessel Is, Gove Peninsula, NT, 11°27.60'S, 136°28.7'E, 32 m, 15 Nov 1990, coll. Hooper, JNA
Z.3946	S W headland, Rimbija I., Cape Wessel, Wessel Is, Gove Peninsula, NT, 11°0.5'S, 136°43.79'E, 15 m, 16 Nov 1990, coll. Hooper, JNA
Z.3956	N side Pugh Shoal, reef slope, NE of Truant I., English Company IS, Gove Peninsula, NT, 11°36.57'S, 136°53.39'E, 20 m, 18 Nov 1990, coll. Hooper, JNA
Z.4078	Near boat ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, coll. B. Glasby & party, by hand
Z.4104	Near boat ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, coll. B. Glasby & party, by hand
Z.4131	Near boat ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, coll. B. Glasby & party, by hand
Z.4197	"Town Hall" hole, SW Channel I., Middle Arm of Darwin Harbour, NT, 12°33.74'S, 130°51.67'E, 19.5 m, 9 Sep 2004, coll. Alvarez, B
Z.4198	Sand Island, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°35.291'S, 130°52.264'E, 7 m, 9 Sep 2004, coll. Alvarez, B
Z.4425	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.09'S, 130°47.1'E, 5–19 m, 8 May 2002, coll. Alvarez, B and party
Z.4428	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.09'S, 130°47.1'E, 5–19 m, 8 May 2002, coll. Alvarez, B and party
Z.4435	Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4–8 m, 6 May 2002, coll. Alvarez, B and party
Z.4448	Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4–8 m, 6 May 2002, coll. Alvarez, B and party
Z.4462	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.21'S, 130°35.46'E, 5–10 m, 26 May 2003, coll. Alvarez, B and party
Z.4463	Rimbija I., 2.8 km W of Cape Wessel, Wessel Is, eastern Arnhem Land, NT, 11°00.21'S, 136°43.84'E, 17–20 m, 1 Apr 2004, coll. Colin, P
Z.4465	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.57'S, 136°17.86'E, 11–20 m, 5 Apr 2004, coll. Alvarez B and party
Z.4486	Raft Point, Bynoe Harbour, NT, 12°37.69'S, 130°32.16'E, 5–8 m, 26 Jun 2003, coll. Alvarez, B and party
Z.4488	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.21'S, 130°35.46'E, 5 m, 1 Jun 2005, coll. Alvarez, B
Z.4490	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17'S, 130°47.19'E, 5 m, 8 May 2006, coll. Alvarez, B
Z.4491	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17'S, 130°47.19'E, 14 m, 8 May 2006, coll. Alvarez, B
Z.5053	South Shell I., East Arm, Darwin Harbour, NT, 12°29.87'S, 130°53.12'E, 4–11 m, 18 Aug 2002, coll. Alvarez, B and party
Z.5054	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.6'S, 136°17.84'E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party

APPENDIX (continued)

Collection and locality data of material examined in the collections of QM and NTM.

NTM material

Z.5055	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.6′S, 136°17.84′E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5057	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.6′S, 136°17.84′E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5058	Raragala I., 700 m off NE tip Wessel Is, eastern Arnhem Land, NT, 11°32.85′S, 136°21.28′E, 13–16 m, 31 Mar 2004, coll. Alvarez, B
Z.5059	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.55′S, 136°17.96′E, 25–30 m, 5 Apr 2004, coll. Alvarez, B and party
Z.5064	Weed Reef, entrance to West Arm, Darwin Harbour, NT, 12°29.25′S, 130°47.54′E, 9–15 m, 3 Aug 2002, coll. Alvarez, B and party
Z.5065	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.24′S, 130°35.56′E, 5–10 m, 23 May 2003, coll. Alvarez, B and party
Z.5066	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.6′S, 136°17.84′E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5067	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.28′S, 136°17.52′E, 13–14 m, 5 Apr 2004, coll. Alvarez B. and party
Z.5068	"Town Hall" hole, SW Channel I., Middle Arm of Darwin Harbour, NT, 12°33.74′S, 130°51.67′E, 10–18 m, 17 Sep 2002, coll. Alvarez, B and party
Z.5071	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.35′S, 130°31.45′E, 6–8 m, 11 Jun 2003, coll. Alvarez, B and party
Z.5072	Weed Reef, entrance to West Arm, Darwin Harbour, NT, 12°29.25′S, 130°47.54′E, 9–12 m, 6 Sep 2003, coll. Alvarez, B
Z.5074	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.49′S, 130°31.29′E, 9–10 m, 11 Jun 2003, coll. Alvarez, B and party
Z.5075	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.6′S, 136°17.84′E, 17–20 m, 30 Mar 2004, coll. Alvarez, B and party
Z.5662	East Point, Darwin Harbour, NT, 12°24.16′S, 130°47.66′E, 11 m depth, 8 November 2008, coll. Ayling, A
Z.5665	East Point, Darwin Harbour, NT, 12°24.16′S, 130°47.66′E, 11 m depth, 8 November 2008, coll. Ayling, A
Z.5816	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.21′S, 130°35.46′E, 3–12 m, 1 Jun 2005, coll. Alvarez, B
Z.5817	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.21′S, 130°35.459′E, 6 m, 27 Apr 2007, coll. Alvarez, B
Z.5818	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.21′S, 130°35.459′E, 6 m, 27 Apr 2007, coll. Alvarez, B
Z.5819	East Point, Fannie Bay, Darwin, Australia, 12° 24.484′S, 130° 48.471., 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5820	East Point, Fannie Bay, Darwin, Australia, 12° 24.484′S, 130° 48.471., 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5821	East Point, Fannie Bay, Darwin, Australia, 12° 24.484′S, 130° 48.471., 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5822	East Point, Fannie Bay, Darwin, Australia, 12° 24.484′S, 130° 48.471., 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5823	East Point, Fannie Bay, Darwin, Australia, 12° 24.484′S, 130° 48.471., 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5824	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5825	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5826	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5827	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5828	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5829	East Point, Fannie Bay, Darwin, NT, 12° 24.49′S, 130° 48.43′E, 14 m, 25 May 2007, coll. Alvarez, B
Z.5830	South Shell I., East Arm, Darwin Harbour, NT, 12°29.87′S, 130°53.14′E, 7–11. m, 19 Aug 2002, coll. Alvarez, B and party
Z.5831	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 17 m, 8 May 2006, coll. Alvarez, B
Z.5832	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 14 m, 8 May 2006, coll. Alvarez, B
Z.5835	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.103′S, 130°47.111′E, 8–14 m, 7 May 2002, coll. Alvarez, B and party
Z.5836	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.071′S, 130°47.103′E, 10–15 m, 9 May 2002, coll. Alvarez, B and party
Z.5839	East Point, Fannie Bay, Darwin, Australia, 12° 24.48′S, 130° 48.47′E, 11 m, 7 Jun 2007, coll. Alvarez, B
Z.5840	East Point, Fannie Bay, Darwin, NT, 12° 24.49′S, 130° 48.43., 14 m, 25 May 2007, coll. Alvarez, B
Z.5841	East Point, Fannie Bay, Darwin, NT, 12° 24.49′S, 130° 48.43., 14 m, 25 May 2007, coll. Alvarez, B
Z.5842	East Point, Fannie Bay, Darwin, NT, 12° 24.49′S, 130° 48.43., 14 m, 25 May 2007, coll. Alvarez, B
Z.5843	Mengalum I., off Kota Kinabalu, Malaysia, 6 10.87′N, 115 35.97′E, 10–13 m, 24 Oct 2005, coll. Alvarez, B
Z.5844	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.103′S, 130°47.111′E, 8–14 m, 7 May 2002, coll. Alvarez, B and party

APPENDIX (continued)

Collection and locality data of material examined in the collections of QM and NTM.

NTM material

Z.5848	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.17′S, 130°47.19′E, 14 m, 8 May 2006, coll. Alvarez, B
Z.5853	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.2′S, 130°35.459′E, 3–12 m depth, 1 June 2005, coll. Alvarez, B
Z.5854	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.2′S, 130°35.459′E, 3–12 m depth, 1 June 2005, coll. Alvarez, B
Z.5855	Stevens Rock, 1.25 km SE Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.103′S, 130°47.111′E, 8–14 m, 7 May 2002, coll. Alvarez, B and party

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Baudina gen. nov., constituting the first record of Pasytheidae from Australia, and Sinoflustridae fam. nov., with a checklist of Bryozoa and Pterobranchia from Beagle Gulf

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ABSTRACT

Baudina gen. nov., comprising two new species from the Beagle Gulf of Australia's Northern Territory, is the first pasytheid bryozoan to be recorded from Australian continental waters. Colonies are wholly encrusting, forming uni- to triserial ramifying colonies. The zooids have the largest gymnocystal perforations of any other pasytheid, living or fossil. The new *Baudina* taxa constitute two of 84 bryozoan species so far known from Beagle Gulf, including Darwin Harbour. *Sinoflustra* Liu and Yang, 1995, a genus of uncertain affinity, is herein designated the type species of a new family, Sinoflustridae, which also includes *Membraniporopsis* Liu in Liu, Yin and Xia, 1999. The bryozoan diversity of the Beagle Gulf is small relative to what may be expected of tropical Indo-Pacific bryozoans for an area this size and it is likely that several hundred more species will be discovered upon further dedicated sampling.

KEYWORDS: Bryozoa, Pasytheidae, Sinoflustridae, new family, *Baudina*, new genus, Beagle Gulf, Darwin, Northern Territory, new genera, new species, taxonomy.

INTRODUCTION

This paper reports upon bryozoans collected in the Beagle Gulf by the former Conservation Commission of the Northern Territory (CCNT). A survey of the invertebrate fauna was made from the western side of Anson Bay (13°29.64′S, 129°51.00′E) to the eastern side of Cape Hotham (12°12.36′S, 131°23.22′E) in October 1993. The survey included 162 stations sampled by dredging in water depths of 4–39 m. Substrata sent to the author for examination included molluscan shell, and coral and bryozoan rubble. These were thoroughly examined for bryozoan diversity and a checklist of species was included as Appendix 3 in the final report of the survey by the then Parks and Wildlife Commission of the Northern Territory (Smit *et al.* 2000).

The bryozoan diversity in the samples is representative of the tropical Indo-Pacific bryozoan fauna, with most of the species covered in the four-volume series on Bryozoa in the Siboga Expedition Reports (Harmer 1915, 1926, 1934, 1957), for example. The most notable taxonomic discovery in the collection was two undescribed species representing a new genus of Pasytheidae, a family of cheilostome bryozoans not previously recorded in Australian continental waters. A forthcoming volume on Australian bryozoans in the Australian Biological Resources Study *Fauna of Australia* series, which aims to be comprehensive in its coverage, necessitates formal description of these new taxa so that they can be included in the *Fauna* volume.

The Pasytheidae currently comprises six genera. All are characterised by perforate gymnocystal frontal walls and the complete absence of ovicells and polymorphs like articulated oral spines and avicularia. Some species have stolons that ramify across the substratum and erect branches arise from these. The new genus discovered in the Beagle Gulf, is striking for the large size of the gymnocystal perforations and one of the two new species has a stout pair of non-articulated horn-like processes adjacent to the orifice. This paper formally describes the new genus and its constituent species and provides a checklist of all known species of bryozoans and pterobranchs in the vicinity of Darwin.

MATERIAL AND METHODS

Specimens collected during the survey were fixed in a 10% formalin-seawater solution on board the chartered fishing vessel *Kunmunyah* and later sorted by staff at the Museum and Art Gallery of the North Territory (NTM), Darwin.

The new bryozoan species described below were studied by scanning electron microscopy (SEM), using type and other specimens. Sorted material was immersed in sodium hypochlorite solution to remove all cuticularised membranes and dried soft parts in preparation for SEM. All

specimens thus prepared were coated in gold-palladium and photographed using a LEO 440 SEM. Measurements of zooids were made directly from specimens using a light microscope (Zeiss Stereomicroscope SV-11) with an eyepiece graticule.

Primary types of the new species are lodged at NTM.

SYSTEMATICS

Order Cheilostomata Busk, 1852
Suborder Neocheilostomina d'Hondt, 1985
Superfamily Hippothooidea Busk, 1859
Family Pasytheidae Davis, 1934
Genus *Baudina* gen. nov.

Type species. *Baudina geographae* sp. nov.

Gender. Feminine.

Diagnosis. Colony encrusting, uni- to pluriserial, ramifying. Zooids with 5–15 relatively large gymnocystal perforations. Orifice circular, no condyles. Horn-like lateral-oral processes present or absent. No polymorphs or ovicells. Ancestrula with imperforate frontal gymnocyst. Budding of zooids lateral and/or distal.

Etymology. The genus name honours Nicolas-Thomas Baudin, captain, explorer and leader of the 1800–1804 expedition of *Géographe* and *Naturaliste* to Australia (Dunmore 1969; Horner 1987; Gordon *et al.* 1998). Baudin's voyage was tragically marred by the deaths of most of the savants on the voyage and by his own death from tuberculosis at Mauritius on the return trip; nevertheless, his expedition returned to Paris one of the most significant natural-history collections ever amassed during a single voyage. Owing to biased reporting of the expedition by François Péron, Baudin's name was deliberately omitted from the official account and his personal achievement was inadequately appreciated for more than a century. Surprisingly, his name has not previously been commemorated in a genus and it is my desire to correct this oversight.

Remarks. *Baudina* is clearly a member of the neocheilostome superfamily Hippothooidea, which comprises the hippothoomorph families Hippothoidae, Chorizoporidae, Trypostegidae and Pasytheidae. Allied with this group is the genus *Haplopoma* Levinsen, 1909. Often included in the lepralioid family Microporellidae (e.g. Hayward and Ryland 1999), it is gymnocystal-shielded and requires its own family. Although relatively character-poor, *Baudina* has distinctive features and the question is, to which of the above taxa is it most closely allied? Hippothoidae and Chorizoporidae are ruled out on two counts – all species in these families have ovicells and lack frontal gymnocystal perforations. Additionally, orifices are sinusoid in Hippothoidae and hemispherical in Chorizoporidae. Both species of *Baudina*, described below, have gymnocystal foramina and circular orifices and lack ovicells. Species of Trypostegidae and *Haplopoma* have gymnocystal perforations, but all genera have ovicells. Additionally, many trypostegids have avicularium-like zooidal polymorphs while *Haplopoma* species have an ascopore and well-developed basal pore-chambers; none of these characters is found in *Baudina*. Taking all characters into consideration, *Baudina* is closest to the Pasytheidae. All genera in this family have perforated frontal shields and lack ovicells and other polymorphs. Further, the orifice is typically weakly sinusoid or subcircular. *Baudina* differs from other pasytheids less in zooidal morphology than in colonial morphology. Pasytheids form ramifying colonies (like *Baudina*) but in these the zooids are mostly proximally attenuated, tending to claviform, are mostly basally jointed, and some species produce erect jointed branches, lacking in *Baudina*. Nevertheless, in general morphology, zooidal rows of *Baudina naturalistae* (below) are most similar to the unjointed linear chains of basal zooids in the pasytheid *Gemellipora eburnea* Smitt (see Gordon 1984; pl. 44A), which differs in the form of the orifice (slightly sinusoid, with condyles) and in having only tiny perforations and erect branches.

The family Pasytheidae currently comprises the genera *Pasythea* Lamouroux, 1812, *Dittosaria* Busk, 1866, *Gemellipora* Smitt, 1873, *Euteleia* Marcus, 1938, *Tecatia* Morris, 1980 and *Unifissurinella* Poignant, 1991, with *Baudina* only the seventh genus to be recognised. *Baudina* differs from all other pasytheid genera in the large size of the gymnocystal foramina; zooids are also proximally unjointed but joints are not universal in Pasytheidae.

Baudina geographae sp. nov.

Figs 1–5

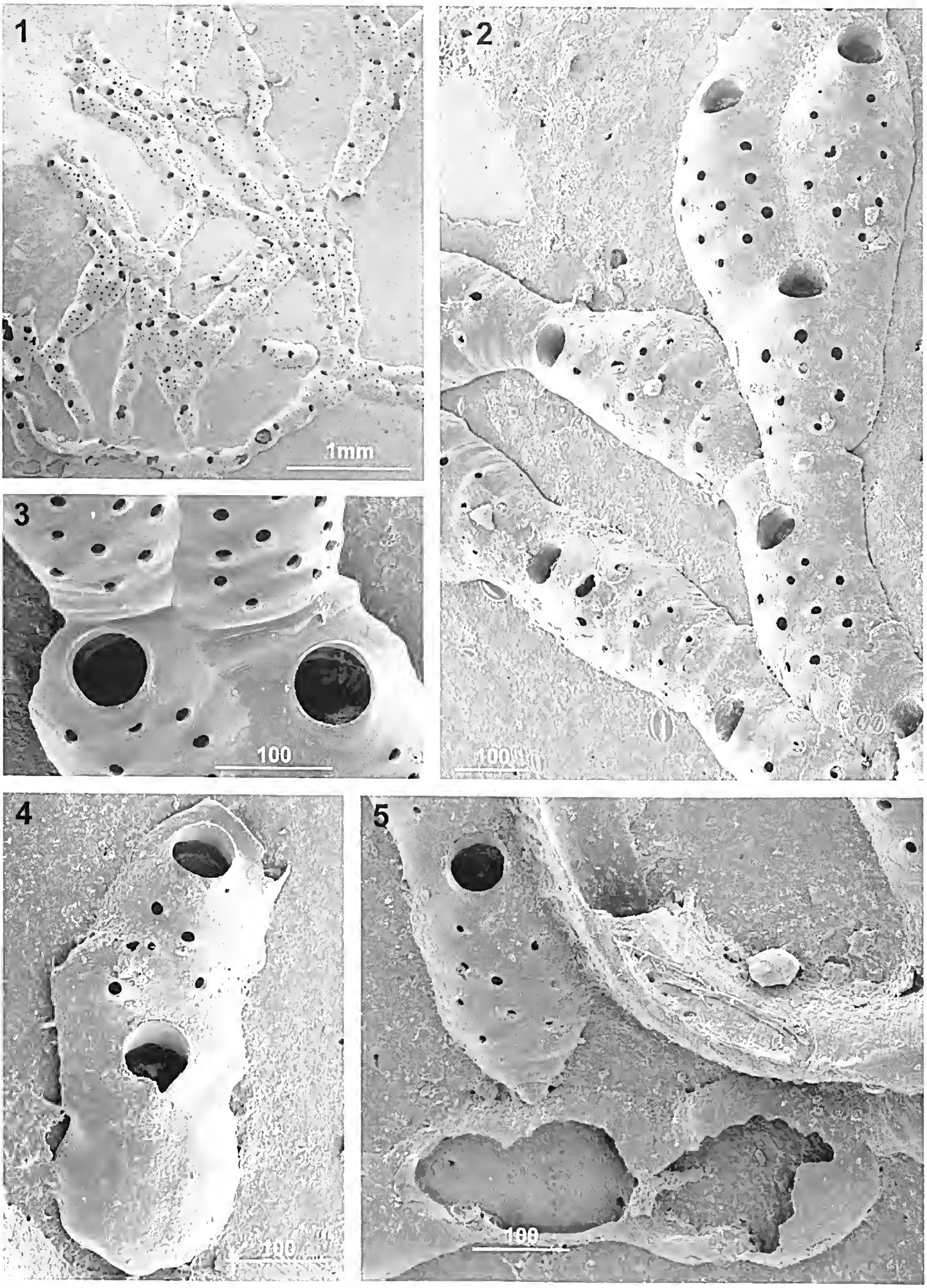
HOLOTYPE – NTM G.273 (unique specimen; no paratypes).

Type locality. CCNT Beagle Gulf station 103, off Charles Point, 12°18.96′S, 130°40.74′E, 23 m depth, attached to the interior surface near the umbo of a dead valve of the spiny oyster *Spondylus victoriae* G.B. Sowerby II, 1869 (Bivalvia: Spondylidae) from a sandy mud and gravel bottom.

Description. Colony encrusting, hyaline and inconspicuous, comprising uni- to pluriserial ramifying chains of zooids not more than 4 zooid rows wide.

Zooids small, 347–438 μm long, 156–224 μm wide, with a smooth frontal shield that may have a slightly undulating surface. Gymnocystal foramina from 6 (post-ancestrular zooid to 15 per zooid, relatively large, 9–19 μm diameter. Orifice circular to slightly subcircular, 57–77 μm diameter, with no condyles or peristome. No articulated spines or avicularia. No ovicells.

Ancestrula 250–262 μm long, 181–200 μm wide, with near-circular orifice 56–67 mm diameter; proximal end rounded, frontal shield smooth, imperforate, merging smoothly with gymnocyst of mid-distal daughter zooid.



Figs 1–5. *Baudina geographae* gen. nov., sp. nov., holotype: **1**, whole colony, showing uni-pluriserial rows of zooids; **2**, part of colony showing bifurcations of zooid rows; **3**, zooidal orifices; **4**, ancestrula (proximal rim of orifice damaged) and daughter zooid; **5**, damaged ancestrula (lower right) and daughter zooid, with a zooid row commencing from a lateral budding site on the daughter zooid. Scale bars in µm for Figs 2–5.

Further budding takes place mid-proximally from ancestrula and mid-distally from first daughter zooid, thus establishing a linear, uniserial chain in both directions; proximal end of daughter zooid originating from both sides of ancestrular orifice. Colony spread achieved by mid-lateral budding of some zooids in chain and by zooid bifurcation of those at each end of chain; zooids budded laterally have shortly tapering proximal ends. Ramifying zooid chains may merge and fuse.

Etymology. The species name alludes to the *Géographe*, one of the vessels of the Baudin expedition. It is intended as a noun in apposition.

Remarks. The unique holotype colony is known only from the type locality where it encrusted a shell fragment.

Baudina naturalistae sp. nov.

Figs 6–10

Holotype – NTM G.274. Paratype – NTM G.275, from same locality as holotype.

Type locality. CCNT Beagle Gulf station 103, off Charles Point, 12°18.96′S, 130°40.74′E, 23 m depth, on the erect branching bryozoan *Nellia tenella* from a sandy mud and gravel bottom.

Description. Colony encrusting, hyaline and inconspicuous, comprising uni- to biserial linear chains of zooids.

Zooids very small, 224–291 µm long, 112–123 µm wide, with very smooth frontal shield. Gymnocystal foramina relatively large, 12–24 µm diameter, 5–6 per zooid, their rims very slightly elevated. Orifice circular, 67–72 µm diameter, no condyles, rim sometimes very slightly elevated. A stout, hollow, non-articulated horn-like process at each distolateral corner of orifice; when fully developed these curve and taper toward each other, almost meeting, forming an arch across orifice. No articulated spines or avicularia. No ovicells.

Budding of zooids occurs distally, with branching occurring through the bifurcation of zooid rows. Ancestrula not seen.

Etymology. The species name alludes to the *Naturaliste*, the second of the vessels of the Baudin expedition that set out from France in 1800. It is intended as a noun in apposition.

Remarks. Colonies encrust erect branching cheilostome bryozoans. Two hosts have been encountered – *Nellia tenella* (Quadricellariidae) and *Scrupocellaria diadema* (Candidae), on both of which *B. naturalistae* may grow down the branch towards the substratum in the opposite growth direction to the host, or it may grow upwards in the same direction. On the latter host, *B. naturalistae* accommodates itself remarkably to the varied surface topography, with individual zooids achieving very twisted profiles (Fig. 10). The species is so far known only from the northeastern corner of Fog Bay to the Vernon Islands east of Cape Hotham at depths of 6 to 23 m.

Order Cheilostomata Busk, 1852a

Suborder Malacostegina Levinsen, 1902

Superfamily Membraniporoidea Busk, 1852b

Family Sinoflustridae fam. nov.

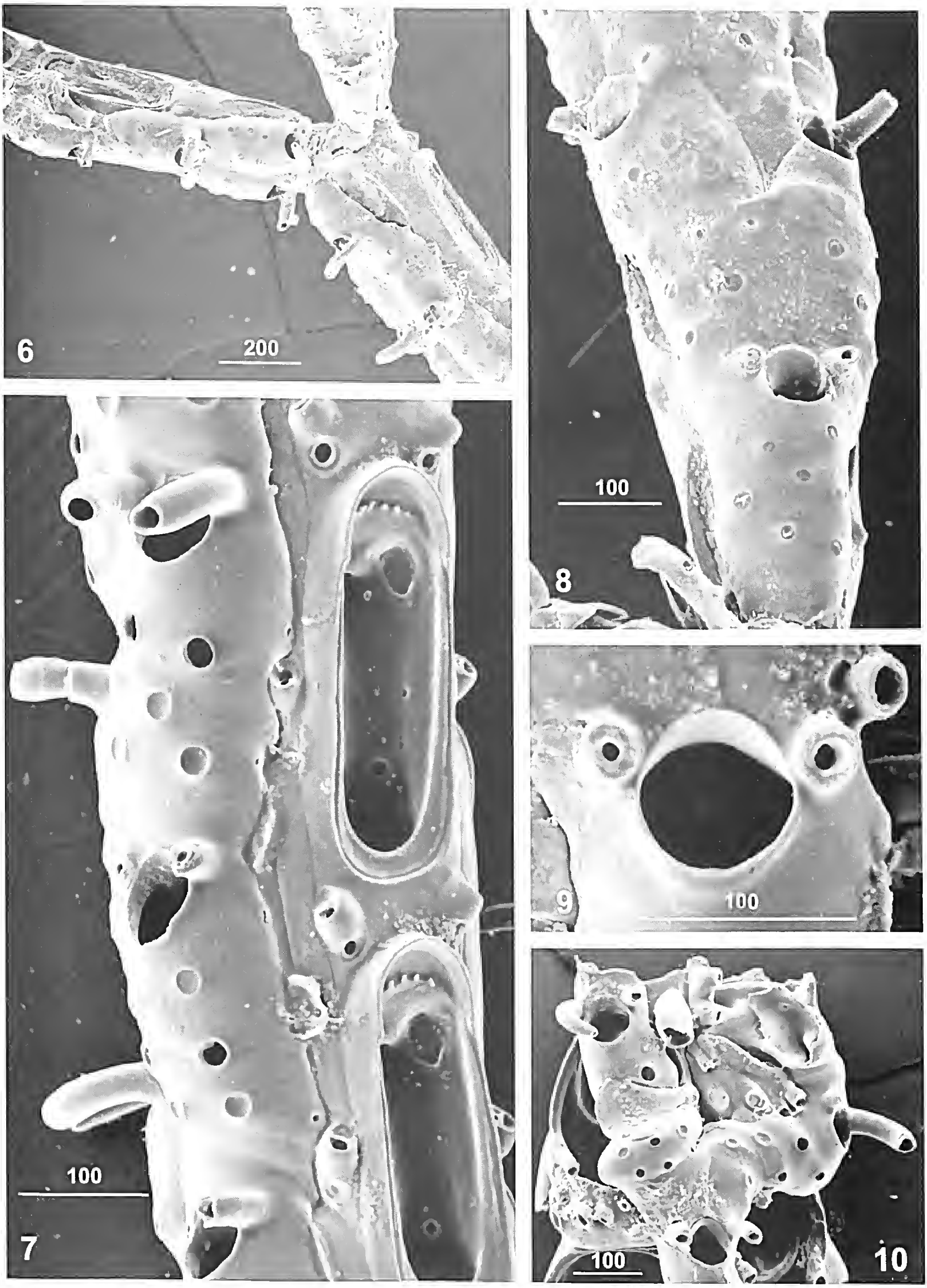
Diagnosis. Colony solely encrusting or producing erect unilaminar or bilaminar lobes or fronds from encrusting base. Zooids elongate-oval (neanic colonies) to rectangular, with a membranous frontal wall occupying entire frontal area. Cryptocyst narrow, usually granular, often developed more proximally and sometimes with horizontal spinous processes around opesia; gymnocyst typically absent but may be present or vestigial in periancestrular and some neanic zooids. Some zooids aviculariform, slightly larger than autozooids, expanded distally with large mandible-like opercula. Paired kenozooids budded distolaterally just below level of cryptocystal shelf but projecting frontalwards, having the form of short funnels or spines, with or without branching processes. Ancestrula single, bearing distolateral kenozooids. Reproduction involves many small ova, larval form unknown.

Type genus. *Sinoflustra* Liu and Yang, 1995.

Remarks. A specimen of *Sinoflustra amoyensis* (Robertson, 1921), the type species of *Sinoflustra*, was found at the Port of Darwin on an anthropogenic substratum in August 2002 and photographs of it were sent to the author for identification. The taxonomic status of this genus, and its family attribution, have been unclear and the opportunity is taken here to clarify the situation.

The species was originally described as *Membranipora amoyensis* by Robertson (1921) from Amoy (Xiamen), China, encrusting a molluscan shell in water of presumed lowered salinity. It has since been found on the west coast of India (Menon and Nair 1967, 1975) and throughout the coast of southern China (Liu 1992) at depths of 0–25 m. Although the zooids of *S. amoyensis* and its congeners are membraniporiform, they have long been recognised as differing substantially in having polymorphs that resemble avicularia, which are otherwise unknown in malacostegine cheilostomes. These polymorphs are slightly larger than regular autozooids and were first described in *Sinoflustra annae* (Osburn, 1953) by Hastings (1930) [as *Acanthodesia serrata sensu* Hastings, non Hincks, 1882], who noted that they have a normal polypide and parietal muscles. *Sinoflustra* species also have a single ancestrula, not twinned as in membraniporids in the strict sense (see Taylor and Monks 1997).

For these reasons, Liu and Yang (1995) established *Sinoflustra*, which they attributed to the neocheilostome family Flustridae. In addition to the type species *S. amoyensis* they also included *A. annae*. There is one other potential species, originally described as *Alderina arabianensis* Menon and Nair, 1975, but Liu and Yang (1995) included it in the synonymy of *S. amoyensis*. Curiously, Menon and Nair (1975) described both "*Membranipora amoyensis*"



Figs 6–10. *Baudina naturalistae* sp. nov. (holotype figs 6–9): **6**, part of uniserial colony growing proximally on host colony of *Nellia tenella*; **7**, close-up of zooids showing diagnostic characters of orificial processes and large gymnocystal foramina; **8**, bifurcation of zooid row; **9**, orifice and bases of orificial processes; **10**, zooids on *Scrupocellaria* host. Scale bars in µm.

and "*Alderina arabianensis*" in the same paper, each well illustrated, attributing them to different genera and families. Liu (1992), Liu and Yang (1995), and Liu *et al.* (2001) have discussed variability in this species, with the degree of calcification evidently related to salinity (Liu 1992); both spinosity (of opesial and kenozooidal spines) and the relative size of the cryptocyst can vary among populations but the precise causes remain unknown.

One other genus may be allied with *Sinoflustra* (Gordon *et al.* 2006), i.e. *Membraniporopsis* Liu in Liu, Yin and Xia, 1999, attributed by its author to the Membraniporidae. Like *Sinoflustra* it has distinctive distolateral kenozooids, but in the two known species of *Membraniporopsis* – *M. bifloris* (Wang and Tung, 1976) and *M. tubigera* (Osburn, 1940) – these are infundibuliform (somewhat funnel-shaped) with short lateral processes, not spine-like. Two other species may be allied with these genera. Although it has not yet been discovered to have avicularium-like polymorphs, *Membranipora serrilamelloides* Liu and Li, 1987 has short spine-like kenozooids like those of *Sinoflustra annae* and hence probably belongs to *Sinoflustra*. *Conopeum truitti* Osburn, 1944 may be a species of *Membraniporopsis*. Osburn (1944) compared it to *M. tubigera*, commenting on the kenozooidal processes in the zooidal corners. They produce only cuticular tubercles frontally and it is not clear from Osburn's illustrations how the kenozooids originate, so the question is open.

Gordon *et al.* (2006) discussed the relationship between *Sinoflustra* and *Membraniporopsis*, concluding that the two genera were obviously closely related but remarked that, in the absence of information about embryos and/or larvae, choice of a family was uncertain (possibly Electridae or Flustridae), and noted that, if it should turn out that either of these genera should have planktotrophic larvae, then a new family should be created to accommodate them. In the event, McCann *et al.* (2007) [who, like Gordon *et al.* (2006), provisionally included *Sinoflustra* in the Flustridae] noted that Karande and Udhayakumar (1992) had also given some information on reproduction in *S. annae* from western India. In Mumbai harbour waters, *S. annae* co-occurs with three other malacostegine species, all of which have relatively large numbers of small eggs, as is typical of forms that produce planktotrophic cyphonautes larvae. Although Karande and Udhayakumar (1992) did not record cyphonautes larvae in the harbour plankton or attribute such larvae to *S. annae*, they noted that reproductive zooids of *S. annae* contained six to seven small eggs. This is conclusive evidence that *Sinoflustra* is a malacostegine cheilostome, not a neocheilostome. Accordingly, a new family, Sinoflustridae, is created here for the constituent genera *Sinoflustra* (two or three species) and *Membraniporopsis* (two or three species). The Sinoflustridae differs from the Membraniporidae chiefly in having a non-twinned ancestrula and from the Electridae in having distinctive polymorphs – the avicularium-like zooids in *Sinoflustra* and the distolateral kenozooids in both genera.

CHECKLIST OF BRYOZOA FROM BEAGLE GULF AND DARWIN HARBOUR

The checklist of species mostly comprises bryozoans collected during the CCNT surveys (station data in Appendix 1), to which have been added *Amphibiobeania epiphylla*, a remarkable endemic genus and species of mangrove epiphyte (Metcalfe *et al.* 2007), plus some alien species reported by Russell and Hewitt (2000) and *Sinoflustra amoyensis*, found in Darwin Harbour on anthropogenic substrata.

There is a range of colonial morphologies. Of the indigenous species, 26 (33%) are two-dimensional encrusters. This is a smaller proportion of this morphology than would be expected for the total range of habitats available in the Darwin region and may be an artifact of sampling or, what is more likely, subsequent sorting of samples sent for analysis. It is usual for visually obvious erect and large bryozoans to be collected in the field by non-bryozoologists, whereas relatively high diversities of small encrusting species can found on dead molluscan shells, and the samples analysed by the author contained very little such material. Ten additional encrusters form more or less inconspicuous ramifying uni–pluriserial colonies. Fifteen species form fixed-erect colonies that may be tree-like, reticulate or planar from a relatively small attachment point. Nine species (mostly species of *Celleporaria* plus *Cigclisula occlusa*) start life as two-dimensional encrusters but soon become mounded and/or erect and coralline owing to frontal budding of zooids that results in thick, rigid multilamellate colonies. Several of the *Celleporaria* species are large and robust, serving as important substrata for other bryozoans. The most important of these are *C. oculata* and *C. fusca*, which resemble small corals – the latter bore 14 other cheilostome species. One striking growth form is free-living (vagrant), with two exemplars in the Darwin area, viz *Cupuladria guineensis* and *Selenaria punctata*, which form discoidal colonies that live on sandy substrata.

Russell and Hewitt (2000) reported five species of alien/cryptogenic bryozoans from the vicinity of the Port of Darwin. *Bugula neritina*, *Savignyella lafontii* and *Watersipora subtorquata* are distinctive and easily recognised; the records of *Amathia distans* and *Zoobotryon verticillatum* need confirming on the basis of voucher specimens in so far as *A. distans* may be confused with native *Amathia* species and *Z. verticillatum* has some similarities to native *Vesicularia papuensis*.

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CHECKLIST OF BRYOZOA OF BEAGLE GULF

(CCNT Beagle Gulf station numbers given for those species collected during the survey)

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULIPORINA Johnston, 1847
Superfamily TUBULIPOROIDEA Johnston, 1838
Family TUBULIPORIDAE Johnston, 1838
Idmidronea sp. BG/95
Family TERVIIDAE Canu and Bassler, 1920
Nevianipora pulcherrima (Kirkpatrick, 1890) BG/95
Suborder ARTICULINA Busk, 1959
Superfamily CRISIOIDEA Johnston, 1838
Family CRISIIDAE Johnston, 1838
Crisia elongata Milne Edwards, 1838 BG/69, BG/95, BG/122, BG/148, BG/153
Class GYMNOLAEMATA Allman, 1856
Order CTENOSTOMATA Busk, 1852
Suborder EUCTENOSTOMATINA Jebram, 1973
Superfamily ARACHNIDIOIDEA Hincks, 1880
Family NOLELLIDAE Harmer, 1915
Nolella papuensis (Busk, 1886) BG/103
Superfamily WALKERIOIDEA Hincks, 1877
Family AEVERRILLIIDAE Jebram, 1973
Aeverrillia setigera (Hincks, 1887) BG/42, BG/67, BG/69
Family WALKERIIDAE Hincks, 1877
Walkeria atlantica (Busk, 1886) BG/27
Superfamily VESICULARIOIDEA Johnston, 1847
Family VESICULARIIDAE Johnston, 1847
Amathia crispa (Lamarck, 1816) BG/26, BG/46, BG/91, BG/95, BG/160
Amathia sp. BG/69
Vesicularia papuensis Busk, 1886 BG/72, BG/73
Order CHEILOSTOMATA Busk, 1852
Suborder INOVICELLINA Jullien, 1888
Superfamily AETEOIDEA Smitt, 1867
Family AETEIDAE Smitt, 1867
Aetea anguina (Linnaeus, 1758) BG/121
Aetea truncata (Landsborough, 1852) BG/103, BG/122
Suborder MALACOSTEGINA Levinsen, 1902
Superfamily MEMBRANIPOROIDEA Busk, 1852
Family MEMBRANIPORIDAE Busk, 1852
Biflustra savartii auctt. BG/38, BG/57, BG/91, BG/119
Jellyella tuberculata (Bosc, 1802) BG/78
Family SINOFLUSTRIDAE fam. nov.
Sinoflustra amoyensis (Robertson, 1921) Port of Darwin
Suborder NEOCHEILOSTOMINA d'Hondt, 1985
Superfamily CALLOPOROIDEA Norman, 1903
Family ANTROPORIDAE Vigneaux, 1949
Parantropora laguncula (Canu and Bassler, 1929) BG/122, BG/160
Family CALLOPORIDAE Norman, 1903
Parellisina curvirostris (Hincks, 1862) BG/38
Family CUPULADRIIDAE Lagaaij, 1952
Cupuladria guineensis (Busk, 1854) BG/27, BG/28, BG/33, BG/49, BG/77, BG/79, BG/91, BG/97, BG/101, BG/105, BG/113, BG/116, BG/117, BG/123
Family QUADRICELLARIIDAE Gordon, 1984
Nellia tenella (Lamarck, 1816) BG/27, BG/36, BG/38, BG/40, BG/54, BG/67, BG/69, BG/73, BG/95, BG/103, BG/116, BG/119, BG/120, BG/126, BG/144, BG/153
Family FLUSTRIDAE Fleming, 1828
Retiflustra cornea (Busk, 1852) BG/78, BG/82, BG/110, BG/111, BG/127, BG/136, BG/150, BG/159, BG/160, BG/161
Superfamily BUGULOIDEA Gray, 1848
Family BEANIIDAE Canu and Bassler, 1927
Amphibiobeania epiphylla Metcalfe, Gordon and Hayward, 2007 Darwin Harbour
Beania regularis Thornely, 1916 BG/38, BG/67, BG/91, BG/95
Family BUGULIDAE Gray, 1848
Bugula neritina (Linnaeus, 1758) Russell and Hewitt 2000 Port Darwin
Bugula robusta MacGillivray, 1869 BG/95, BG/137
Bugula vectifera Harmer, 1926 BG/95
Family EPISTOMIIDAE Gregory, 1893
Synnotum aegyptiacum (Audouin, 1826) BG/160
Synnotum pembaense Waters, 1913 BG/122
Family CANDIDAE d'Orbigny, 1851
Caberea lata Busk, 1852 BG/48, BG/67, BG/69, BG/73, BG/84, BG/95
Scrupocellaria curvata Harmer, 1926 BG/88, BG/144
Scrupocellaria diadema Busk, 1852 BG/38, BG/40, BG/48, BG/69, BG/84, BG/88, BG/91, BG/95, BG/97, BG/103, BG/113, BG/116, BG/119, BG/121, BG/135, BG/141, BG/160
Scrupocellaria longispinosa Harmer, 1926 BG/95, BG/103
Scrupocellaria spatulata (d'Orbigny, 1851) BG40, BG/95
Superfamily MICROPOROIDEA Gray, 1848
Family CHLIDONIIDAE Busk, 1884
Crepis verticillata Harmer, 1926 BG/91, BG/93, BG/95, BG/103, BG/106, BG/120, BG/121, BG/144, BG/153
Family SELENARIIDAE Busk, 1854
Selenaria punctata Tenison-Woods, 1880 BG/27, BG/47, BG/49, BG/97
Family STEGINOPORELLIDAE Hincks, 1884
Steginoporella dilatata Harmer, 1926 BG/27, BG/127, BG/158

Family THALAMOPORELLIDAE Levinsen, 1909
Thalamoporella novaehollandiae (Haswell, 1880) BG38
Superfamily CELLARIOIDEA Lamouroux, 1821
Family CELLARIIDAE Lamouroux, 1821
Cellaria punctata (Busk, 1852) BG/40, BG/69, BG/95
Suborder ASCOPHORINA Levinsen, 1909
Superfamily CRIBRILINOIDEA Hincks, 1879
Family CRIBRILINIDAE Hincks, 1879
Puellina sp. BG/97
Superfamily CATENICELLOIDEA Busk, 1852
Family CATENICELLIDAE Busk, 1852
Catenicella uberrima Harmer, 1957 BG/67, BG/69, BG/95, BG/103, BG/116, BG/121, BG/137
Family SAVIGNYELLIDAE
Savignyella lafontii (Audouin, 1826) Russell and Hewitt 2000 Port Darwin
Superfamily HIPPOTHOOIDEA Busk, 1859
Family HIPPOTHOIDAE Busk, 1859
Hippothoa calciophilia Gordon, 1984 BG/95, BG/103, BG/119
Family PASYTHEIDAE Davis, 1934
Baudina geographae Gordon, described herein BG/103
Baudina naturalistae Gordon, described herein BG/69, BG/95, BG/103, BG/106, BG/119, BG/122, BG/144, BG/153
Superfamily LEPRALIELLOIDEA Vigneaux, 1949
Family LEPRALIELLIDAE Vigneaux, 1949
Celleporaria aperta (Hincks, 1882) BG/119
Celleporaria discoidea (Busk, 1881) BG/85, BG/91, BG/92, BG/94, BG/97, BG/113, BG/121
Celleporaria fusca (Busk, 1854) BG/38, BG/103, BG/113, BG/121
Celleporaria granulosa (Haswell, 1880) BG/38
Celleporaria oculata (Lamarck, 1816) BG/38, BG/40, BG/48, BG/69, BG/84, BG/88, BG/119, BG/121, BG/122, BG/136, BG/141, BG/144
Celleporaria sibogae Winston and Heimberg, 1986 BG/38, BG/40, BG/46, BG/84, BG/85, BG/92, BG/95, BG/103, BG126, BG/127, BG/160
Celleporaria tridenticulata (Busk, 1881) BG/144
Celleporaria sp. BG/121
Superfamily ADEONOIDEA Busk, 1884
Family ADEONIDAE Busk, 1884
Adeona foliifera Lamarck, 1816 BG/26, BG/81, BG/84, BG/88, BG/93, BG/95, BG/97, BG/99, BG/103, BG/114, BG/119, BG/120, BG/131, BG/143, BG/144
Adeonella intricaria Busk, 1884 BG/50, BG/72, BG/78, BG/83, BG/88, BG/95, BG/103, BG/127, BG/152, BG/160
Adeonella lichenoides (Lamarck, 1816) BG/27, BG/38, BG/40, BG/50, BG/69, BG/80, BG/81, BG/82, BG/95, BG/119, BG/124, BG/147
Superfamily SCHIZOPORELLOIDEA Jullien, 1883
Family SCHIZOPORELLIDAE Jullien, 1883
Schizobrachiella subhexagona (Ortmann, 1890) BG/103, BG/119
Stylopoma duboisii (Audouin, 1826) BG/103
Thornelya perarmata Harmer, 1957 BG/36
Family HIPPOPODINIDAE Levinsen, 1909
Hippopodina feegeensis (Busk, 1884) BG/121, BG/122
Family CHEILOPORINIDAE Bassler, 1936
Cheiloporina haddoni (Harmer, 1902) BG/38
Family LANCEOPORIDAE Harmer, 1957
Calyptotheca australis (Haswell, 1880) BG/38, BG/91, BG/103, BG/119, BG/121, BG/142
Calyptotheca inaequalis Harmer, 1957 BG/103
Calyptotheca wasinensis (Waters, 1913) BG/38, BG/88, BG/92, BG/93, BG/95, BG/122, BG/126
Calyptotheca sp. BG119, BG/121, BG/126, BG/152
Family COLATOOECIIDAE Winston, 2005
Cigclisula occlusa (Busk, 1884) BG/38, BG/69, BG/78, BG/91, BG/95, BG/126, BG/136, BG/144, BG/160
Family PORINIDAE d'Orbigny, 1852
Porina longicollis (Canu and Bassler, 1929) BG/69
Porina vertebralis (Stolickza, 1865) BG/38, BG/40, BG/42, BG/57, BG/67, BG/87, BG/144
Family MARGARETTIDAE Harmer, 1957
Margaretta tenuis Harmer, 1957 BG/40, BG/148
Family PETRALIELLIDAE Harmer, 1957
Hippopetraliella dorsiporosa (Busk, 1884) BG/40, BG/95, BG/97
Mucropetraliella loculifera Harmer, 1957 BG/38, BG/48, BG/95, BG/103, BG/132, BG/136
Mucropetraliella serrata (Livingstone, 1926) BG/95
Petraliella arafurensis Stach, 1936 BG/81
Superfamily SMITTINOIDEA Levinsen, 1909
Family SMITTINIDAE Levinsen, 1909
Parasmittina hastingsae Soule and Soule, 1973 BG/91
Parasmittina vacuramosa Lu, Nie and Zhong MS *in* Lu, 1991 BG/38, BG/48, BG/91, BG/113, BG/116, BG/119, BG/121, BG/122, BG/124, BG/126, BG/132
Family WATERSIPORIDAE
Watersipora subtorquata (d'Orbigny, 1852) Russell and Hewitt 2000 Port Darwin
Superfamily MAMILLOPOROIDEA Canu and Bassler, 1927
Family CLEIDOCHASMATIDAE Cheetham and Sandberg, 1964
Characodoma laterale (Harmer, 1957) BG/92
Superfamily CELLEPOROIDEA Johnston, 1838
Family CELLEPORIDAE Johnston, 1838
Turbicellepora sp. BG/69, BG/95

Family PHIDOLOPORIDAE Gabb and Horn, 1862

Iodictyum gibberosum (Buchner, 1924) BG/121, BG/149

Reteporella graeffei (Kirchenpauer, 1869) BG/40, BG/46, BG/89, BG/103, BG/148

Reteporella granulata (MacGillivray, 1869) BG/149

Rhynchozoon bifurcum Harmer, 1957 BG/38, BG/78, BG/97, BG/142, BG/152, BG/160

Rhynchozoon incrassatum (Hincks, 1882) BG/67, BG/92

Schedocleidochasma porcellaniforme Soule, Soule and Chaney, 1991 BG/91

Triphyllozoon benemunitum (Hastings, 1932) BG/36, BG/38, BG/39, BG/40, BG/46, BG/48, BG/50, BG/52, BG/67, BG/69, BG/71, BG/81, BG/92, BG/93, BG/95, BG/97, BG/121, BG/129, BG/132, BG/136, BG/137, BG/140, BG/141, BG/142, BG/154, BG/155, BG/156, BG/158

Triphyllozoon hirsutum (Busk, 1884) BG148

Triphyllozoon tubulatum (Busk, 1884) BG/40, BG/103, BG/121

Phylum HEMICHORDATA Bateson, 1885
Class PTEROBRANCHIA Lankester, 1877
Order RHABDOPLEURIDA Fowler, 1893
Family RHABDOPLEURIDAE Harmer, 1905

Rhabdopleura annulata Harmer, 1905 BG/121, BG/126, BG/144

DISCUSSION

The total of 84 bryozoan species in the Beagle Gulf samples is small relative to what may be expected of tropical Indo-Pacific bryozoans for an area this size and it is likely that several hundred more species will be discovered upon further dedicated sampling. Indeed, this is true of the Australian tropical and subtropical bryozoan fauna as a whole. Based on the published literature, Gordon and Bock (2008) cited only 319 species for the entire Great Barrier Reef Province and Torres Strait, whereas perhaps a thousand species may be expected on the basis of what is known about bryozoan species diversity in the tropical Indo-Pacific generally. The finding of a new genus with two new species in the same small area is likely to be indicative of further such finds that will follow from more detailed faunal analysis.

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APPENDIX: CCNT BEAGLE GULF (BG) STATION DATA

(All samples collected 3–9 October 1993)

Stn No.	Location	Latitude S	Longitude E	Depth (m)	Substratum
26	Anson Bay	13°16.08	129°55.92	23	Coarse sand, shale, gravel
27	Anson Bay	13°15.90	129°58.86	19	Coarse sand
28	Anson Bay	13°15.96	130°01.86	20	Coarse sand, shale
33	Anson Bay	13°13.26	130°01.92	9	Coarse sand, shale
36	Anson Bay	13°10.26	129°55.62	15	Coarse sand, shale
38	Anson Bay	13°09.24	130°05.52	20	Barnacle-encrusted gravel
39	Peron Islands	13°07.08	129°56.04	15	Coarse sand, mud
40	Peron Islands	13°06.96	129°58.86	8	Fine mud, rocks
42	Peron Islands	13°04.44	129°56.10	14	Coarse sand, shale
46	Peron Islands	13°00.90	129°58.92	14	Coarse sand, shale
47	Peron Islands	13°00.96	130°01.92	17	Coarse sand, shale
48	Peron Islands	13°00.06	130°04.98	13	Mud, shale, sand
49	Peron Islands	13°57.90	130°01.92	16	Mud
50	Peron Islands	13°57.96	130°04.98	10	Sandy mud
52	Fog Bay	12°54.96	130°07.98	7	Mud, shale
54	Fog Bay	12°54.96	130°15.60	4	Sandy mud
57	Fog Bay	12°51.96	130°14.10	7	Mud, shale
67	Bynoe Harbour	12°40.92	130°33.12	9	Coarse sand, shale
69	Fog Bay	12°40.02	130°19.92	6	Mud
71	Grose Islands	12°36.96	130°16.98	13	Mud
72	Port Patterson	12°35.76	130°26.22	3	Fine sand, silt
73	Port Patterson	12°37.08	130°28.08	14	Mud
77	Port Patterson	12°33.60	130°27.90	16	Sandy mud, gravel
78	Bynoe Harbour	12°34.02	130°32.04	28	Coarse sand, shale, gravel
79	Grose Islands	12°31.02	130°14.04	19	Sand
80	Grose Islands	12°31.02	130°17.22	17	Coarse sand, shale, gravel
81	Grose Islands	12°31.02	130°20.04	15	Gravel (sponge bed)
82	Grose Islands	12°30.96	130°22.92	9	Coarse sand, gravel
83	Bynoe Harbour	12°31.02	130°28.98	28	Sandy mud, gravel
84	Bynoe Harbour	12°31.20	130°31.74	11	Coarse sand, gravel
85	Grose Islands	12°27.96	130°20.16	19	Coarse sand, shale, mud
87	Grose Islands	12°27.90	130°26.70	6	Coarse sand
88	Bynoe Harbour	12°28.02	130°28.98	38	Mud, gravel, rocks
89	Bynoe Harbour	12°28.80	130°32.10	14	Mud, gravel
91	Grose Islands	12°25.44	130°25.92	19	Mud, gravel
92	Bynoe Harbour	12°24.84	130°28.92	17	Coarse sand, gravel
93	Bynoe Harbour	12°24.96	130°31.98	29	Sandy mud
94	Charles Point	12°21.96	130°28.74	34	Mud, gravel
95	Charles Point	12°21.90	130°31.92	15	Gravel (sponge bed)
97	Charles Point	12°21.84	130°37.86	14	Coarse sand, shale
99	Darwin Harbour	12°22.14	130°43.98	20	Sandy mud, shale
101	Charles Point	12°19.02	130°34.02	19	Sand, gravel, mud
103	Charles Point	12°18.96	130°40.74	23	Sandy mud, gravel
105	Darwin Harbour	12°19.02	130°47.10	15	Muddy sand, shale, seagrass
106	Darwin Harbour	12°19.08	130°50.04	12	Mud, gravel, shale
110	Charles Point	12°15.84	130°37.86	27	Sandy mud
111	Charles Point	12°16.08	130°40.98	28	Sandy mud
113	Darwin Harbour	12°15.84	130°47.22	20	Sandy mud, shale
114	Darwin Harbour	12°16.08	130°50.04	18	Mud, gravel, shale
116	Shoal Bay	12°15.96	130°55.86	13	Sandy mud, seagrass
117	Shoal Bay	12°16.08	130°58.98	9	Mud
119	Darwin Harbour	12°12.90	130°47.04	23	Mud
120	Darwin Harbour	12°13.02	130°50.04	22	Coarse sand, shale, mud

APPENDIX: CCNT BEAGLE GULF (BG) STATION DATA (continued)

(All samples collected 3–9 October 1993

121	Shoal Bay	12°13.02	130°52.92	19	Mud
122	Shoal Bay	12°13.08	130°55.98	17	Sandy mud, sparse seagrass
123	Shoal Bay	13°13.02	130°58.98	13	Sandy mud
124	Adam Bay	13°12.36	131°12.72	6	Sandy mud, shale, gravel
126	Darwin Harbour	13°10.08	130°46.92	30	Mud, gravel
127	Darwin Harbour	13°10.02	130°49.86	27	Coarse sand, shale, mud
129	Shoal Bay	13°09.96	130°56.10	15	Gravel
131	Gunn Point	12°09.36	131°08.22	4	Sandy mud
132	Adam Bay	12°10.02	131°11.40	4	Sandy mud, shale, gravel
135	Chambers Bay	12°09.84	131°23.22	7	Mud
136	Shoal Bay	12°06.90	130°49.92	18	Sponge bed
137	Shoal Bay	12°07.02	130°52.92	20	Sponge bed
140	Vernon Islands	12°06.90	131°04.80	13	Coral rubble
141	Vernon Islands	12°07.02	131°07.02	20	Large rock
142	Adam Bay	12°06.90	131°11.04	11	Gravel
143	Adam Bay	12°07.02	131°13.98	9	Mud, shale, gravel
144	Chambers Bay	12°07.08	131°20.04	22	Shale, coral rubble
147	Vernon Islands	12°04.02	131°58.86	33	Shale, gravel
148	Vernon Islands	12°03.96	131°01.92	25	Large rock
149	Vernon Islands	12°04.98	131°08.40	26	Gravel, shale, sand
150	Vernon Islands	12°03.96	131°11.10	22	Gravel
152	Cape Hotham	12°04.02	131°20.04	21	Shale
153	Cape Hotham	12°04.08	131°22.80	6	Sponge bed
154	Vernon Islands	12°01.02	130°58.86	30	Rocky bottom
155	Vernon Islands	12°01.02	131°01.86	38	Shale, gravel
156	Vernon Islands	12°01.20	131°03.96	22	Coarse sand, shale, rocks
158	Vernon Islands	12°01.08	131°11.04	20	Gravel, sand
159	Cape Hotham	12°01.32	131°13.92	34	Coarse sand, shale
160	Cape Hotham	12°00.96	131°16.92	29	Coarse sand, shale, gravel
161	Cape Hotham	12°00.96	131°19.86	22	Coarse sand, shale

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A new species and new records of the anthozoan commensal genus *Alcyonosyllis* (Polychaeta: Syllidae: Syllinae)

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ABSTRACT

A new species of *Alcyonosyllis* (Polychaeta: Syllidae), *A. hinterkircheri*, is described from a scleractinian coral, *Goniopora* cf. *stokesi* Edwards and Haime (Poritidae) from shallow coastal waters near Bohol Island, Philippine Islands. It represents the first record of an *Alcyonosyllis* species on a scleractinian coral and the first record of a commensal polychaete on a *Goniopora* species. The new polychaete differs from other described species of *Alcyonosyllis* in having long, slender dorsal cirri exhibiting a strong, long-short alternation pattern over the entire body; in its olive-green colour pattern; and that all chaetae are unidentate. Also, new records of the type species of the genus, *A. phili* Glasby and Watson, 2001, from Australia and the Philippine Islands extend the known range of this species. Lastly, a possible new species from Sumba, Indonesia, similar to *A. xeniaecola* (Hartmann-Schröder, 1993) is mentioned but not formally described because only one specimen is known to date. A dichotomous key is provided to distinguish the seven species known with certainty in the genus.

KEYWORDS: Annelida, Polychaeta, Syllidae, Alcyonosyllis, coral, octocoral, taxonomy, systematics, symbiotic, aquarium.

INTRODUCTION

The anthozoan commensal polychaete genus *Alcyonosyllis* Glasby and Watson, 2001 is so far only known from the Indo-west Pacific and the Red Sea. Five species are presently known, all from octocorals. The type species, *A. phili* Glasby and Watson, 2001 occurs on soft corals of the family Nephtheidae and gorgonians (*Melithaea* sp., family Melithaeidae) and it is known from the tropical northern half of Australia and New Guinea; *A. gorgoniacolo* (Sun and Yang, 2004) from an unidentified orange-red gorgonian from Chenhang Islands, Paracel Group, South China Sea [nation disputed]; *A. glasbyi* San Martín and Nishi, 2003 from Izu Peninsula, Japan, is also commensal with a *Melithaea* species; *A. xeniaecola* (Hartmann-Schröder, 1993) from Maluku, Indonesia, is commensal on the octocoral *Xenia*; and *A. bisetosa* (Hartmann-Schröder, 1960) from Gubal, Red Sea, from an octocoral. The genus could contain further species having compound chaetae in addition to the characteristic simple hooks, including *Syllis onkylochaeta* Hartmann-Schröder, 1991, *Syllis exiliformis* Imajima, 2003 and other similar species currently assigned to *Syllis* (*sensu* San Martín and Nishi, 2003; Aguado *et al.*, 2008). However, in this paper we will only consider those species that coincide with the type species *A. phili* in having only simple chaetae.

Recent collections by Johann Hinterkircher in 2004 and 2008 in shallow coastal waters around Bohol Island, Philippine Islands, have yielded an undescribed *Alcyonosyllis* species living on a scleractinian coral, *Goniopora* cf. *stokesi* Edwards and Haime (Poritidae). The specimens are herein described as a new species. The 2004 collecting trip also yielded a specimen of *Alcyonosyllis phili*, commensal on a gorgonian, making this the northern-most record for this species. Other specimens of *A. phili* from northern Australia, previously misidentified as belonging to the Pilargidae in the collection of the Museum and Art Gallery of the Northern Territory, Darwin, are also reported and new information is provided on the distribution and habitat of this species. In addition, a specimen of *Alcyonosyllis* from Sumba, Indonesia, collected on the Dutch-Indonesian Snellius II Expedition (1984–1985) to Indonesian waters is also described; although it resembles *A. xeniaecola*, it possibly represents a new species, but further material is required before formally naming it.

Given the occurrence of all species of *Alcyonosyllis* on both octocorals and scleractinian corals, it is likely that further specimens of existing and new species, will be collected by persons within the aquarium trade. Images of *Alcyonosyllis* species on their hosts in aquaria are already circulating among these persons (Leslie Harris pers. comm.), but unfortunately species of *Alcyonosyllis* cannot be recognised by colour pattern alone and definitive identification will require examination of appropriately preserved specimens.

MATERIAL AND METHODS

All specimens were fixed in a 10% formaldehyde-seawater solution and preserved in a 70% ethanol solution. Observations were made using an Olympus SZ30 stereomicroscope and an Olympus CH30 compound microscope. Drawings were made to scale, with a camera lucida drawing tube on a Nikon Optiphot microscope equipped with differential interference contrast optics (Nomarsky). Observations on *A. hinterkircheri* were made using a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse 80i compound microscope with Nomarsky optics and photographs were made on both microscopes using a Qimaging Micropublisher 5.0 RTV digital camera.

The width of specimens was measured at the level of the proventricle, excluding parapodia. One paratype (NTM W.23000) of *A. hinterkircheri* sp. nov. was dissected ventrally in order to describe features of the anterior gut. The studied material is deposited at the Museum and Art Gallery of the Northern Territory, Darwin (NTM; formerly Northern Territory Museum) and the Museum of Natural History, Naturalis, Leiden (RMNH; formerly Rijks Museum van Natuurlijke Historie). Comparative material on loan from the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF) and the Zoologisches Museum, Universität Hamburg, Hamburg (HZM) was also examined.

TAXONOMY

Family Syllidae Grube, 1850

Subfamily Syllinae Grube, 1850

Genus *Alcyonosyllis* Glasby and Watson, 2001

Gender feminine. Type species, by original designation, *Alcyonosyllis phili* Glasby and Watson, 2001. Recent. Indo-west Pacific Ocean.

Diagnosis. Syllinae with long body and large number of chaetigers. Prostomium with 2 pairs of eyes, 3 antennae; palps free to base. Nuchal organs as inconspicuous ciliated ridge between prostomium and tentacular segment. Two pairs of tentacular cirri. Antennae, tentacular-, dorsal-, and anal cirri unarticulated to weakly articulated. Dorsal cirri showing typical syllid length-alternation pattern, LSSLSLSSLSLSLSLS…, with long (L) type displaced dorsally and sometimes substantially thicker than short ones. Ventral cirri present, extending short of, or beyond, parapodial lobes. Parapodia uniramous, bearing 1 or 2 types of subacicular simple hook chaetae, both with subdistal boss. One to several aciculae per parapodium, tapered or distally rounded. Pygidium with paired anal cirri. Pharynx with single anterodorsal tooth and 10 ciliated terminal papillae; trepan absent. Reproduction by schizogamy, single stolons attached to parental body in posterior (= terminal) position; parent regenerates new posterior end ventral to the stolon prior to its detachment.

Remarks. The diagnosis of the genus is broadened slightly in this work to account for the weakly articulated dorsal cirri in the new species described below. *Alcyonosyllis* and *Haplosyllides* are among a few Syllinae genera that do not have strongly articulated dorsal cirri, a feature considered to be the result of a reversal to the plesiomorphic condition by Aguado and San Martín (2009). In the occurrence of simple chaetae only in parapodia, *Alcyonosyllis* resembles *Haplosyllis, Haplosyllides, Parahaplosyllis* and *Trypanoseta* and some species of *Syllis*; however, as the form of the simple chaetae differs significantly between these taxa, it is highly likely that each has acquired them independently, and that those in *Alcyonosyllis* represent an adaptation to symbiosis with a cnidarian host. In addition, stolons of *Alcyonosyllis* are attached terminally to the parental body (Glasby and Watson 2001; San Martín and Nishi 2003; Aguado and San Martín 2009) and a new posterior end is regenerated ventrally to the stolon before its release (Fig. 3D). This ability has been reported only in four other Syllinae: *Haplosyllis*, *Megasyllis*, *Parahaplosyllis* and *Trypanosyllis* (Martin *et al.* 2002; Aguado and San Martín 2009). In most Syllinae, stolons appear terminally but the posterior end does not regenerate until the stolon is detached. Glasby and Watson (2001) list several other differences between *Alcyonosyllis* and other syllid genera that have simple chaetae. The following key provides a means of identifying all species currently known in the genus including *A. gorgoniacolo*, which was recently transferred from *Haplosyllis* by Lattig and Martin (2009).

Key to species of *Alcyonosyllis*

1a. A single chaeta (occasionally 2) of 1 type per parapodium .... *A. glasbyi*
1b. More than one chaeta (usually 2–4), of 2 types per parapodium 2

2a. Dorsal cirri highly dimorphic (longer ones very thick and arising higher on dorsum than short ones); several aciculae per parapodium 3
2b. Dorsal cirri all slender, though may differ slightly in length and elevation; 1–2 aciculae per parapodium 4

3a. Each parapodium with 1–3 chaetae; smaller types with minute subdistal tooth................................. *A. phili*
3b. Each parapodium with 3–5 chaetae; smaller types without subdistal tooth................. *A. gorgoniacolo**

4a. Dorsal cirri with strong length-alternation pattern over whole body; dorsal cirri weakly articulated (most obvious anteriorly) 5
4b. Dorsal cirri on posterior chaetigers more or less same length (greater than body width); dorsal cirri smooth .... *A. xeniaecola*

5a. Large species; chaetae all unidentate; 2–6 aciculae .... *A. hinterkircheri* sp. nov.

5b. Small species; some chaetae bidentate; 1–2 aciculae.. 6

6a. Bidentate chaetae with subdistal tooth just below primary tooth; aciculae in anterior parapodia very large................*Alcyonosyllis* sp. (mentioned below)

6b. Bidentate chaetae with subdistal tooth well below primary tooth (1/3 way to boss); aciculae in anterior parapodia not enlarged ....*A. bisetosa*

* This is the correct spelling of this specific name. We believe the specific name *gorgoniacolo* was intended as a noun in apposition by Sun and Yang (2004: 313) and could not have been a lapsus or printer's error at the point of first introduction (which might have been grounds for emending it) since it is spelt consistently in this same form in four other places in the original description. Accordingly, the change to *gorgoniacola* (sic) by Lattig and Martin (2009: 37) is not followed here.

Alcyonosyllis hinterkircheri sp. nov.

(Figs 1–3, 4A, Table 1)

Material examined. Holotype – Philippine Islands, Panglao Island, south-west of Bohol Island, Alona Beach 3 km from Panglao City (9°34.683'N, 123°44.75'E), 1–4 m, coll. Johann Hinterkircher, 4 October 2004, NTM W.22998 Paratypes – same collection details as for holotype, 1 (NTM W.22999); same location as holotype but 0.5–1.5 m, coll. Johann Hinterkircher, October 2008, 3 (NTM W.23000).

Description (based on holotype, except where indicated otherwise). Holotype 53 mm long, 0.13 mm wide, with 178 segments; developing female stolon at rear end. Paratypes 88–102 mm long, 1.3–1.5 mm wide, with 194–242 segments; one paratype (NTM W.23000) with well-developed female stolon at rear of body. Body of similar width throughout, tapering over first and last several segments. Dorsum highly convex, venter more or less flat. Body pigmentation (olive green in life, faded to light brown in ethanol) restricted to dorsal surface of broad intersegmental furrows (Fig. 1A,B). Distinctive yellow-white glandular region between segmental furrows, becoming elevated in mid and posterior chaetigers. In life, worms well camouflaged against coral host, ranging from 100–200 mm long (Fig. 1A; Johann Hinterkircher pers. comm.).

Prostomium broader than long, rectangular to ovate, with 2 closely-set pairs of eyes in trapezoidal arrangement, anterior pair larger than posterior pair. Palps broad, basally free, longer than prostomium (Fig. 2A–C). Median antenna inserted on middle of prostomium, weakly articulated, approximately 2.5 times length of lateral antennae. Lateral antennae inserted on anterior part of prostomium, weakly articulated, similar in length to combined length of prostomium and palps. Peristomium slightly shorter than anterior segments. Dorsal tentacular cirri weakly articulated,

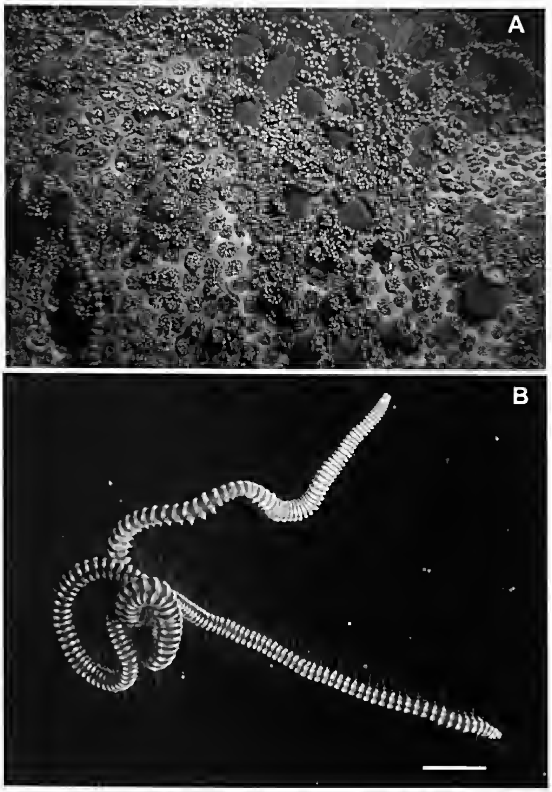

Fig. 1. *Alcyonosyllis hinterkircheri* sp. nov, **A**, Several individuals *in situ* on *Goniopora* cf. *stokesi* at Panglao Island, near Bohol Island, Philippine Islands. Note that most coral polyps are retracted. Photo: J. Hinterkircher. **B**. Paratype (NTM W.22999) alive, removed from host. Head at bottom right. Photo: J. Hinterkircher. Scale: 5.0 mm.

similar in length to median antennae; twice length of ventral pair (Fig. 2C).

Parapodia comprising dorsal and ventral cirri and broad parapodial lobe; pre-chaetal lip slightly more prominent than post-chaetal lip throughout. Dorsal cirri weakly articulated, more so distally, of two distinct forms: longer, dorsally-displaced ones on chaetigers 1, 4, 6, 9, 11 and thereafter on odd chaetigers (Fig. 3B,D), and shorter laterally-directed ones arising closer to parapodial lobes on chaetigers 2, 3, 5, 7, 8, 10 and thereafter on even chaetigers (Fig. 3A,C). Longest dorsal cirri in midbody up to 2.5 x body width; shorter ones about $^1/_2$–$^1/_3$ length of longer ones. Ventral cirri smooth, approximately $^1/_2$ length of parapodial lobe anteriorly, equal in length to parapodial lobe in mid and posterior chaetigers (Figs 2B, 3D).

Parapodia each bearing two types of unidentate hooked chaetae, thicker prominently hooked type, and thinner, less hooked type, both with subdistal boss (Fig. 3F,G); chaetae sometimes withdrawing into parapodium (Fig. 3E); four chaetae per parapodium (n = 4), some paratypes with only two chaetae per parapodium – one thick, one thinner. Neuroaciculae straight, with slight subdistal swelling, varying in number from 6 (anteriorly) to 2 (posteriorly) (Fig. 3E). Single, slender, notopodial acicula

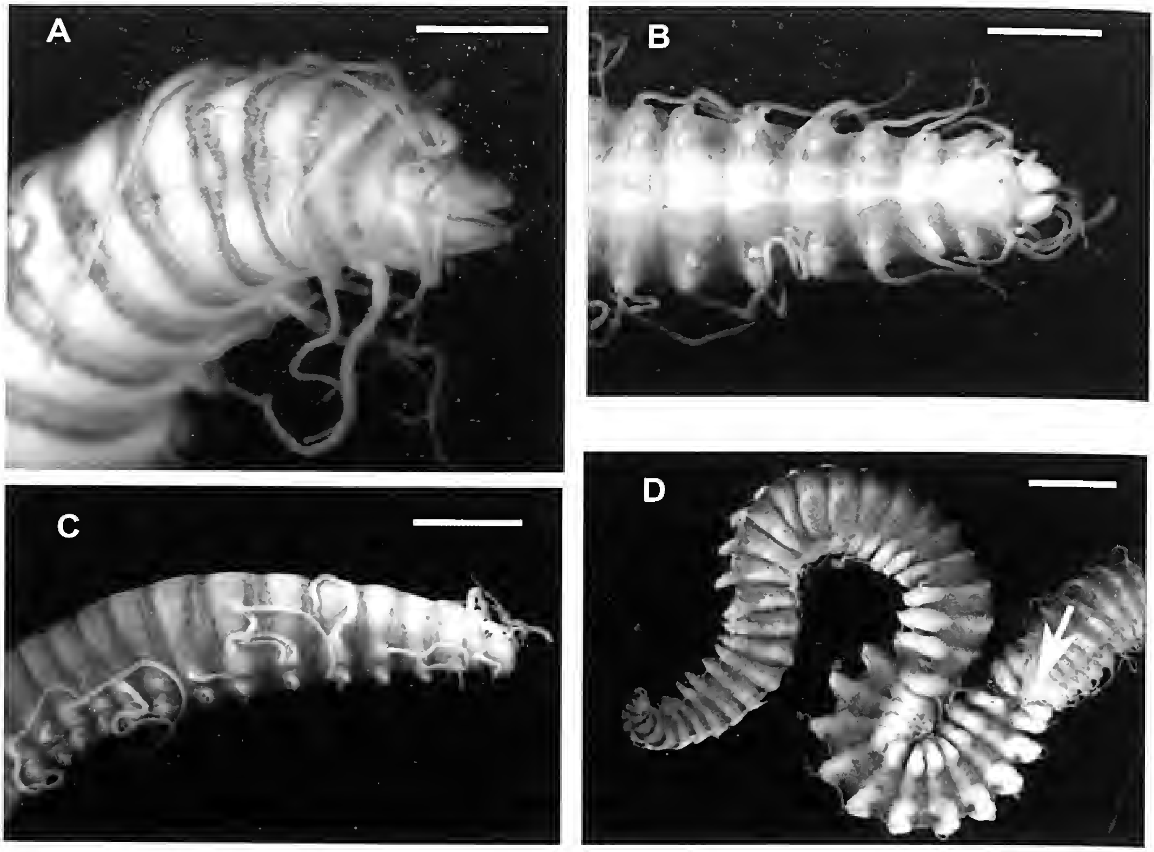

Fig. 2. *Alcyonosyllis hinterkircheri* sp. nov. preserved specimen. **A**, Holotype, anterior end, dorsal view; **B**, Holotype, anterior end, ventral view; **C**, Holotype, anterior end, lateral view; **D**, Paratype (NTM W.2300), posterior end, showing developing stolon and regenerating pygidium of parent (indicated with arrow). Scale A–D: 1.0 mm.

in each posterior parapodium most likely associated with developing schizogamous stolon.

Pygidium swollen, slightly upturned and bearing a pair of long slender weakly articulated cirri on ventral edge (Fig. 1B). One paratype (NTM W.23000) with well-developed female stolon attached to posterior body; at point of attachment stock developing new tail end ventrally (Fig. 2D).

Pharynx retracted and together with proventricle not visible through body wall. Pharynx short (about $^2/_3$ length proventricle) extending to anterior chaetiger 4, relatively thick (about $^2/_3$ width proventricle) and slightly coiled with curved, anterodorsal hyaline tooth (Fig. 4A). Number and form of distal papillae could not be determined on dissected pharynx. Proventricle extending from anterior of chaetiger 4 to posterior of chaetiger 7, with about 25 muscle rows (Fig. 4A).

Remarks. The new species is generally similar to *A. phili* in having multiple aciculae and two or more chaetae per parapodium of two different types. It differs from this species and all other *Alcyonosyllis* species in: (1) having longer, more slender dorsal cirri with a strong long-short alternation pattern until the pygidium; (2) that its antennae and pygidial cirri are also longer and more slender; (3) having an olive-green banding colour pattern (*A. phili* has red-brown bands), although this may reflect the colour of the host; (4) that the thinner of the two hooked chaetae lacks the secondary (subdistal) tooth; and (5) that the ventral cirri are about half the length of the parapodial lobe anteriorly and equal in length to the parapodial lobe in mid and posterior chaetigers (see also Table 1).

Etymology. The species is named in honour of the collector, Johann Hinterkircher, of Munich in Germany, a keen underwater photographer and collector who has donated many interesting polychaete specimens to the NTM.

Distribution. Presently only known from the Philippine Islands (Panglao Island, south-west of Bohol Island).

Habitat. As many as 20–50 individuals of *Alcyonosyllis hinterkircheri* were found on a single *Goniopora* cf. *stokesi* coral according to Johann Hinterkircher (pers. comm. 24 March 2006). In life, the polychaetes were well hidden at the bases of the long polyps of the host, and the colour pattern and shape of the polychaetes matched closely that of the coral making them difficult to see. When the coral was disturbed and the polyps withdrawn, the polychaetes

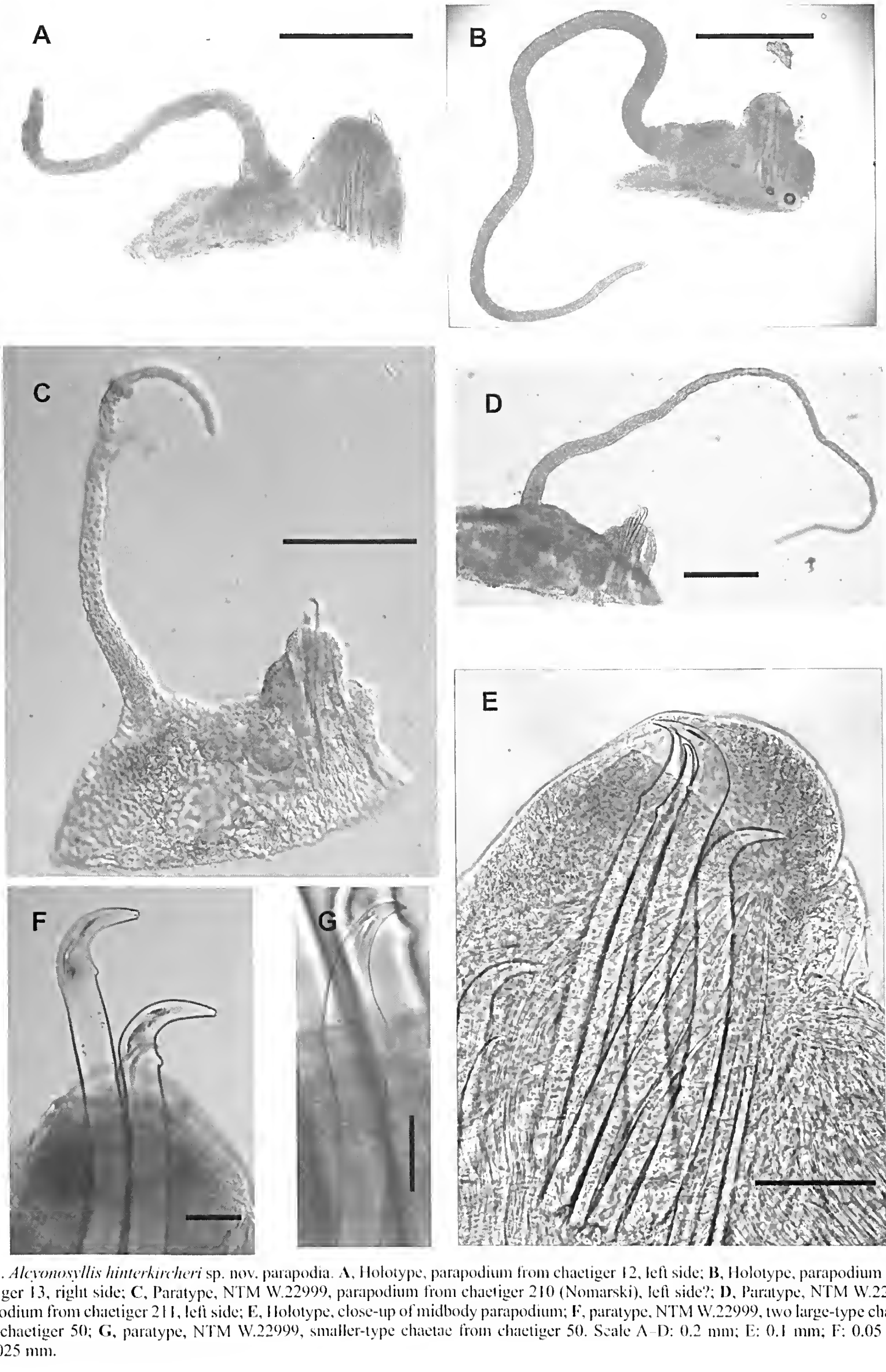

Fig. 3. *Alcyonosyllis hinterkircheri* sp. nov. parapodia. **A**, Holotype, parapodium from chaetiger 12, left side; **B**, Holotype, parapodium from chaetiger 13, right side; **C**, Paratype, NTM W.22999, parapodium from chaetiger 210 (Nomarski), left side?; **D**, Paratype, NTM W.22999, parapodium from chaetiger 211, left side; **E**, Holotype, close-up of midbody parapodium; **F**, paratype, NTM W.22999, two large-type chaetae from chaetiger 50; **G**, paratype, NTM W.22999, smaller-type chaetae from chaetiger 50. Scale A–D: 0.2 mm; E: 0.1 mm; F: 0.05 mm; G: 0.025 mm.

could be easily seen (Fig. 1A). Although scleractinians like *Goniopora* are not closely related to octocorals (the most common hosts of *Alcyonosyllis*), their long polyps perhaps make them similar both structurally and functionally to the typical octocoral hosts.

Among the many associations between polychaetes and cnidarians, this appears to be the first record of a commensal polychaete on a species of *Goniopora* (see Martin and Britayev 1998). Further, this is the first record of an *Alcyonosyllis* species associated with a scleractinian coral.

Alcyonosyllis phili Glasby and Watson, 2001

(Table 1)

Alcyonosyllis phili Glasby and Watson, 2001: 45–49, figs 1–5.

Material examined. Philippine Islands, Bohol Island, Alona Beach 3 km from Panglao City (9°34.683′N, 123°44.75′E), 15 m, coll. Johann Hinterkircher, 3 September 2003, 1 (NTM W.23001). Australia, Darwin Harbour, East Arm Port 1 (NTM W.4175), 1 (NTM W4176), 2 (NTM W.4178), 2 (NTM W.4231), Casuarina Beach 1 (NTM W.4230), Nightcliff 5 (NTM W.4244), Timor Sea, Ashmore Reef, 21 m depth 1 (NTM W.4991).

Remarks. The single specimen of *A. phili* from Bohol, Philippine Islands, which was found on a gorgonian, agreed well with the material from Australia and New Guinea described by Glasby and Watson (2001). The specimen from Ashmore Reef was commensal on a sea fan. The Darwin Harbour specimens from East Arm Port were all collected from reef flat sediments (coarse sand); all were relatively small (< 10 mm long), which suggests that young forms may be free-living. The specimens from Bohol Island and Ashmore Reef are the northern and western-most records, respectively, for the species.

Alcyonosyllis sp.

(Figs 4B, 5A–F; Table 1)

Material examined. 1 (RMNH 21117). NE coast of Sumba (9°57'S 120°48'E), sandy bottom with unidentified sponges and gorgonians, 50 m, 1.2 m Agassiz trawl, 16 September 1984. Snellius II expedition.

Comparative material. *Haplosyllis xaeniaecola* Hartmann-Schröder, 1993: Holotype (SMF4431/1) Ternate, Moluccas, Indonesia, on *Xenia viridis* Schenk. *Haplosyllis bisetosa* Hartmann-Schröder, 1960: Holotype (HZM P-14745), Djubal, Red Sea, 1 m on alcyonarian, coll.

Table 1. Comparative list of selected characters for the *Alcyonosyllis* species having simple chaetae, together with information on host, distribution and literature reference.

Species	Length (mm)	Dorsal cirri	Large-type hooks (greatly curved)	Small-type hooks (gently curved)	Aciculae (no.)	Host(s)	Distribution	References
A. phili Glasby and Watson, 2001	28–56	Smooth; elevated ones thicker than non-elevated ones	present	present, minute secondary tooth	3–5	soft corals (Neptheidae), gorgonian (*Melithaea* sp: Melithaeidae)	Philippines, New Guinea, northern Australia	Glasby and Watson (2001); this study
A. xaeniaecola (Hartmann-Schröder, 1993)	15	Smooth; all same thickness	present	present, unidentate	?	soft coral (*Xenia viridis*: Xeniidae)	Ternate (Maluku I.), Moluccas, Indonesia	Hartmann-Schröder (1993), Glasby and Watson (2001)
A. glasbyi San Martín and Nishi, 2003	16	Weakly articulated; all same thickness	absent?	present; minute secondary tooth	1	gorgonian (*Melithaea flabellifera*: Melithaeidae)	Shimoda, Japan	San Martín and Nishi (2003)
A. hinterkircheri sp. nov.	100–200	Weakly articulated; all same thickness	present	present, unidentate	2–6	hard coral (*Goniopora* cf. *stokesi*)	Bohol, Philippines	This study
Alcyonosyllis sp.	7	Weakly articulated; all same thickness	present	present, bidentate	1–2	gorgonian	Sumba, Indonesia	This study
A. bisetosa (Hartmann-Schröder, 1960)	5.8	Weakly articulated; all same thickness	present	present, secondary tooth	2	soft coral	Gubal, Red Sea	Hartmann-Schröder (1960); San Martín and Nishi (2003); Lattig and Martin (2009)
A. gorgoniacolo (Sun and Yang, 2004)	75–85	Smooth; elevated ones thicker than non-elevated ones	present	present, minute secondary tooth absent	3–4	Orange-red gorgonian	Chenhang Island, Paracel Group, South China Sea	Sun and Yang (2004); Lattig and Martin (2009)

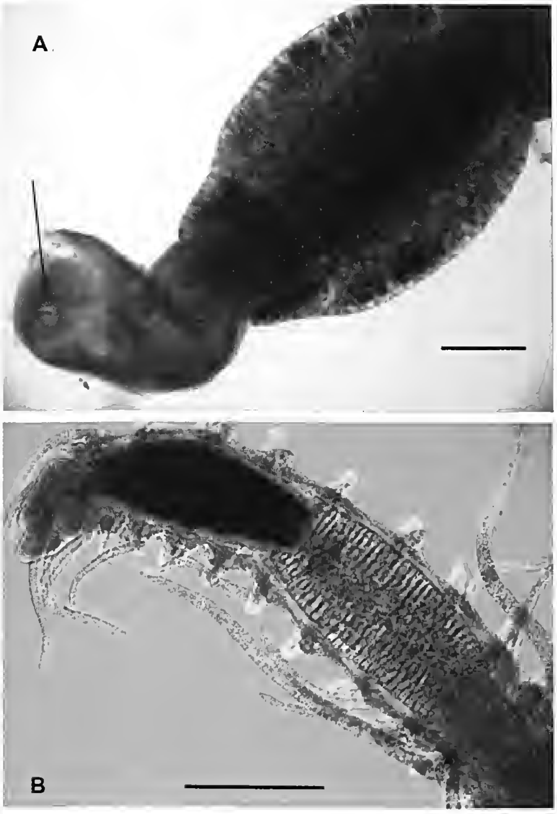

Fig. 4. A. *Alcyonosyllis hinterkircheri* sp. nov. Paratype, NTM W.23000, pharynx and proventricle dissected out to show anterodorsal tooth (indicated by arrow); **B,** *Alcyonosyllis* sp. Anterior end, dorsal view. Note muscle rows of proventricle and weakly articulated anterior dorsal cirri. Scale A: 0.5 mm; B: 0.3 mm.

Gerlach, 29 October 1957; ?paratype 1 (HZM unregistered), collection details as for holotype.

Description. Specimen 7 mm long, 0.5 mm wide, with 38 segments (posteriorly incomplete). Dorsum convex and venter flat. Body unpigmented, whitish; pharynx red (Fig. 4B). Anterior segments without marked intersegmental furrows; after proventricular chaetigers, segments well delimitated, with secondary posterior ring (Fig. 5A,E). Prostomium broader than long, rectangular to oval, with 2 pairs of eyes in trapezoidal arrangement, posterior ones larger than anterior ones. Palps broad, close-set basally, longer than prostomium. Median antenna inserted on middle of prostomium, weakly articulated, approximately twice as long as lateral antennae. Lateral antennae inserted on anterior part of prostomium, weakly articulated, as long as combined length of prostomium and palps (Figs 4B, 5A). Peristomium shorter than subsequent segments (Fig. 5A). Dorsal tentacular cirri weakly articulated, as long as median antennae; twice as long as ventral pair.

Dorsal cirri slender and distally tapering, anterior ones weakly articulated, those from mid- and posterior body less so (Figs 4B; 5A,E), with granular material inside. Anterior dorsal cirri alternating in length, some of them extremely long, those from chaetiger 15, about 12 segments in length. Shortest anterior dorsal cirri slightly longer than body width. Midbody and posterior dorsal cirri alternating in length, but distally shorter than anterior ones, longest cirri about 5 segments in length and twice length of short ones (Fig. 5E). Some parapodia with less difference in length between both types of dorsal cirri, but still alternating. Cirrophores present on all chaetigers, from midbody onward as distinct constricted ring (Fig. 5F). Ventral cirri digitiform, slightly extending beyond tips of parapodia (Fig. 5F).

Anterior parapodia with 2 simple bidentate chaetae, similar in size, distally curved with both teeth similar in length and size (Fig. 5B). Midbody parapodia with 3 simple chaetae, 2 similar to anterior ones, third hook-shaped, unidentate, distally curved, larger than others (Fig. 5C). Posterior parapodia with 3 chaetae, similar in shape to those from midbody (Fig. 5D); sometimes only 1 bidentate chaeta and 2 unidentate hooked chaetae; hooked chaetae larger than midbody ones and more curved distally. Anterior parapodia with 1 large acicula, orange coloured, straight and distally pointed (Fig. 5B). Midbody and posterior parapodia with 2 aciculae, smaller than anterior ones, 1 straight and pointed, the other distally bent (Fig. 5C, D).

Pygidium missing. Pharynx extending through four segments, narrower than proventricle, with 1 conical anterodorsal tooth (Fig. 5A). Proventricle extending through 4 segments, with about 31 rows of muscle cells (Figs 4B, 5A).

Remarks. *Alcyonosyllis* sp. resembles *Alcyonosyllis xaeniaecola* in having a strongly pigmented red-coloured pharynx. However, all the chaetae in *A. xaenicola* are unidentate, whereas the slender, less hooked, chaetae in *Alcyonosyllis* sp. are bidentate. In addition, *A. xaenicola* has smooth dorsal cirri, while the anterior-most ones in *Alcyonosyllis* sp. are weakly articulated and gradually become smoother towards the posterior end. The presence of weakly articulated anterior dorsal cirri also occurs in *A. hinterkircheri*, which differs from *Alcyonosyllis* sp. in the shape of chaetae and number of chaetae and aciculae. *Alcyonosyllis* sp. differs from *A. bisetosa* in having the smaller chaetae with bidentate hooks with the two apical teeth very close together (Table 1).

Pharyngeal colour has not been considered before as a diagnostic character for syllid species, since it could depend on the preservation state and time spent in ethanol, and it could also be related to their habitat. For instance, several specimens of *Haplosyllis* found in the same sample as *Alcyonosyllis* sp. also had a strongly red-coloured pharynx. Therefore, *Alcyonosyllis* sp. and *A. xaeniaecola* probably acquired the colouration independently, perhaps as a result of similar diets.

Although *Alcyonosyllis* sp. might be a new species, only one specimen is known to date. Therefore, until more material is collected and studied, we prefer not to formally name the species.

Distribution. Moluccas, Savu Sea (Indonesia).

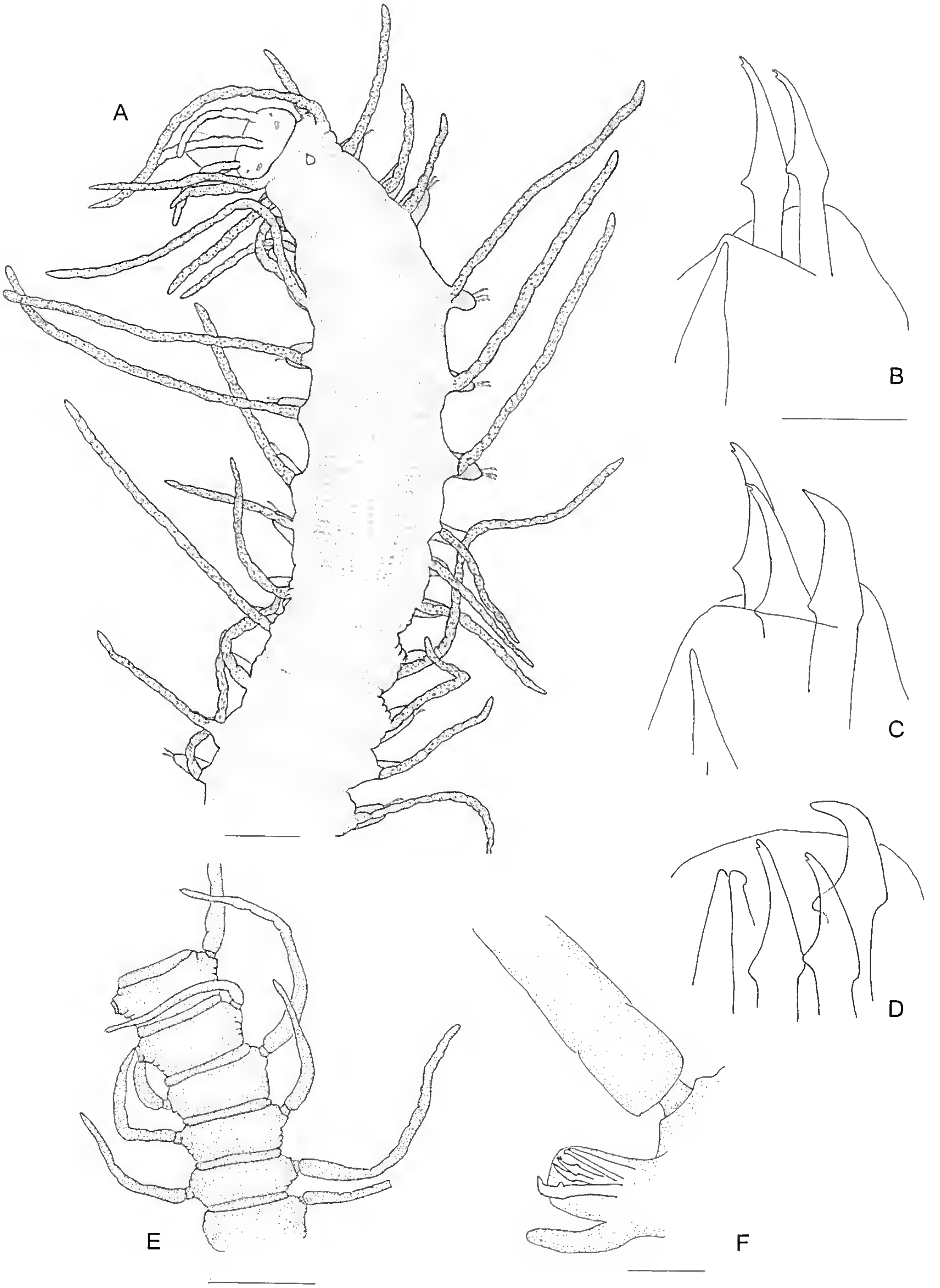

Fig. 5. *Alcyonosyllis* sp. **A**, Anterior end, dorsal view; **B**, Anterior parapodium; **C**, Midbody parapodium; **D**, Posterior parapodium; **E**, Midbody segments, dorsal view; **F**, Midbody parapodium, anterior view. Scale **A**: 0.2 mm; **B–D**: 20 μm; **E**: 0.4 mm; **F**: 48 μm.

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We gratefully acknowledge the help of Carden Wallace in the identification of the scleractinian coral host of the new species, Vivian Wei for translating the description of *Haplosyllis gorgoniacolo* given by Sun and Yang (2004), Richard Willan for clarifying the derivation of the species name *gorgoniacolo*, Harry A. ten Hove for the loan of the specimen from Indonesia, and Dieter Fiege for lending us comparative material. Also, we thank Daniel Martin and an anonymous reviewer for constructive reviews, and Leslie Harris for information on *Alcyonosyllis* occurrences in aquaria. This project was partly financed by the European Commission's Research Infrastructure Action via the SYNTHESYS Project, financed by European Community Research Infrastructure Action under the FP6 'Structuring the European Research Area' Programme.

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The genus *Floresorchestia* (Amphipoda: Talitridae) in tropical Australia

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ABSTRACT

The widespread Indo-West Pacific and Caribbean talitrid genus *Floresorchestia* is reported from Australia for the first time and a new species, *F. australis*, is described. *Floresorchestia australis* is known from pebble beaches in Darwin Harbour, Northern Territory, Australia.

KEYWORDS: Crustacea, Amphipoda, Talitridae, Australia, taxonomy, new species, *Floresorchestia australis*.

INTRODUCTION

Lowry and Springthorpe (2009a) recently described *Talorchestia brucei* from sandy beaches in Darwin, Northern Territory, Australia. A second talitrid species, living on pebble beaches also in Darwin, has since come to our attention. It is described here as *Floresorchestia australis*. This is the first record of the widespread Indo-west Pacific and Caribbean genus *Floresorchestia* Bousfield in Australia.

There are now five tropical talitrid genera known from Australia: *Chelorchestia* Bousfield, 1984 (see Serejo 2009); *Chroestia* Marsden and Fenwick, 1984; *Floresorchestia* Bousfield, 1984; *Microrchestia* Bousfield, 1984 (see Serejo 2009; Lowry and Peart In press); and *Talorchestia* Dana, 1852 (see Serejo 2009). *Chelorchestia* has five species distributed between north-eastern Australia, the eastern Pacific and the Caribbean Sea. *Microrchestia* (five species) appears to be a Papua New Guinea and tropical-warm temperate eastern Australian endemic genus. *Chroestia* (monotypic) appears to be endemic to tropical-warm temperate eastern Australia. *Talorchestia* (eight species, *sensu stricto*) is a widespread Indo-west Pacific tropical endemic genus. *Floresorchestia* (15 species) is also widespread on Indo-west Pacific tropical islands, but like *Chelorchestia* it also occurs in the tropical Caribbean Sea.

Bousfield (1984) recognised *Floresorchestia* for a group of described species with unique stridulating organs on the epimera. Recently Miyamoto and Morino (2008) and Lowry and Springthorpe (2009b) have both discussed the morphology of the genus, refining characters and describing additional new species. In this paper we report the genus from Australia for the first time and describe a new species, *F. australis*, from Darwin, Northern Territory, Australia.

MATERIAL AND METHODS

The description was generated from a DELTA (Dallwitz 2005) database to world talitrid genera and species. Material is lodged in the Museum and Art Gallery of the Northern Territory (NTM; formerly Northern Territory Museum), Darwin and the Australian Museum (AM), Sydney. The following abbreviations are used on the plates: C, coxa; EP, epimeron; G, gnathopod; MD, mandible; MP, maxilliped; OOST, oostegite; P, pereopod; T, telson; U, uropod; OR, outer ramus.

SYSTEMATICS

Family Talitridae

Floresorchestia Bousfield, 1984

Gender feminine. Type species, by original designation, *Orchestia floresiana* Weber, 1892. Recent, Flores Island, Indonesia.

Remarks. For the most recent diagnosis of the genus and a complete list of species see Lowry and Springthorpe (2009b).

Floresorchestia australis sp. nov.

(Figs 1–4)

Type material. Holotype – NTM Cr.16878, male, 8.5 mm, near the boat ramp, Nightcliff, Darwin, Northern Territory, Australia (12°22.759′S 130°50.487′E). Paratypes – NTM Cr.16879, ovigerous female, 9.16 mm; NTM Cr.13149, male, 9.16 mm; NTM Cr.13149, male, 7.4 mm; NTM Cr.16882, 5 males, 4 females; AM. P.80701, 1 male, 1 female, same locality.

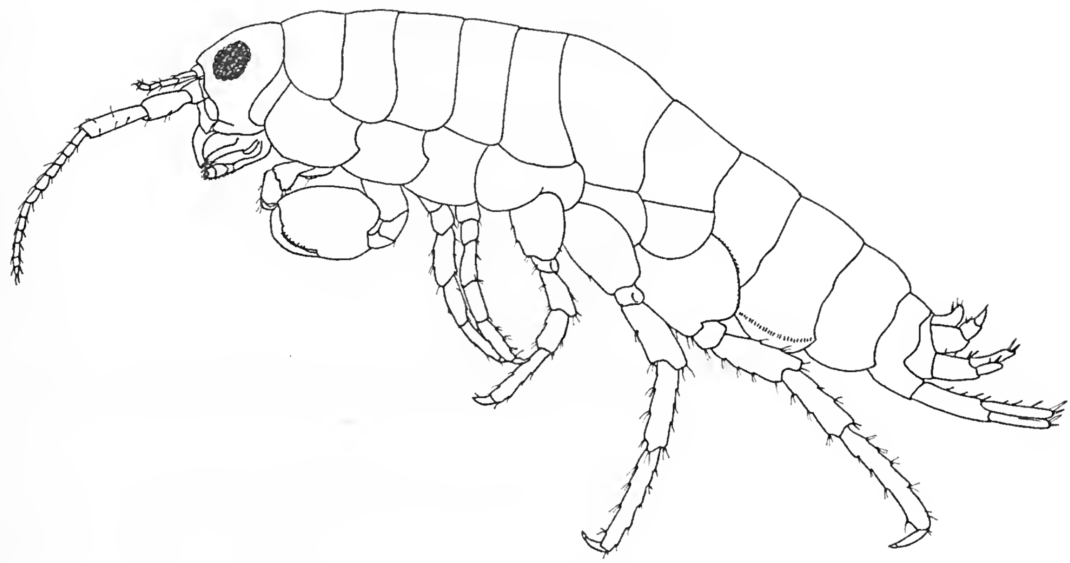

Fig 1. *Floresorchestia australis* sp. nov., paratype, male (NTM Cr.16881).

Type locality. Near the boat ramp, Nightcliff, Darwin, Northern Territory, Australia (12°22.759′S 130°50.487′E).

Etymology. Named for the country to signal the presence of this wide ranging genus in Australia.

Description. Based on holotype, male, 8.5 mm, NTM Cr.16878.

Head. Eye large (greater than 1/3 head length). Antenna 1 short, rarely longer than article 4 of antenna 2 peduncle. Antenna 2 peduncular articles narrow; article 5 longer than article 4. Mandible left lacinia mobilis 4-dentate. Maxilliped palp article 2 distomedial lobe well developed, 4 reduced, button-shaped.

Pereon. Gnathopod 1; subchelate; smaller than coxa 2; posterior margin of merus, carpus and propodus each with lobe covered in palmate setae; propodus 'subtriangular' with well developed posterodistal lobe, anterior margin with 2 groups of robust setae, lateral surface with 3 cuspidate seta, posterolateral surface with 4 serrate setae, medial surface without cuspidate setae, with 5 or 6 serrate setae, posterior margin without cuspidate or serrate setae; palm transverse, with about 7 serrate setae; dactylus slightly longer than palm. Gnathopod 2 sexually dimorphic; subchelate; basis slightly expanded; ischium with anterodistal cradle; posterior margin of merus, carpus and propodus each without lobe covered in palmate setae; propodus subovate, 1.5 times as long as wide; palm extremely acute, reaching less than 60% along posterior margin, smooth, lined with robust setae; posteromedial surface of propodus with groove; with cuticular patch at corner of palm; dactylus longer than palm, attenuated distally; gill simple, not incised. Pereopods 2–4 coxae wider than deep. Pereopods 3–7 cuspidactylate; dactyli with distal patch of many rows of tiny denticles on anterior margin. Pereopod 4 dactylus thickened proximally with notch midway along posterior margin. Pereopod 5 propodus distinctly longer than carpus. Pereopods 6–7 longer than pereopods 3–5. Pereopod 6 not sexually dimorphic; carpus not expanded. Pereopod 7 not sexually dimorphic; basis lateral sulcus absent, posterior margin with distinct minute serrations, each with 1 small seta, posterodistal lobe present, shallow, broadly rounded; distal articles (merus and carpus) slender; merus posterior margin evenly rounded.

Pleon. Pleopods all well developed. Pleopod 1 peduncle with marginal slender and robust setae; biramous, outer ramus subequal in length to peduncle, with 8 articles. Pleopod 2 and 3 biramous. Epimera 2 subequal in length to epimeron, 3 with stridulating organ just above ventral margins, with 31 ridges. Epimeron 3 posterior margin smooth, with minute setae, posteroventral corner with small subacute tooth, ventral margin without robust setae. Uropod 1 not sexually dimorphic, peduncle with 11 robust setae, peduncle distolateral robust seta present, small (less than 1/4 length of outer ramus), with simple tip, without apical spear-shaped setae; inner ramus subequal in length to outer ramus, with 4 marginal robust setae; outer ramus with 1 long midmedial seta, 1 robust seta on margins. Uropod 2 not sexually dimorphic; peduncle with 6 robust setae; inner ramus subequal in length to outer ramus; outer ramus with 1–2 marginal robust setae. Uropod 3 peduncle with 2 robust setae; ramus subequal in length to peduncle, linear (narrowing), with 2 marginal robust setae, ramus with 4–5 apical setae. Telson about as broad as long, completely incised, partially coalesced, dorsal midline entire, with marginal and apical robust setae, with 5 robust setae per lobe.

Female (sexually dimorphic characters). Based on ovigerous female, 9.16 mm, NTM Cr.16879. Gnathopod

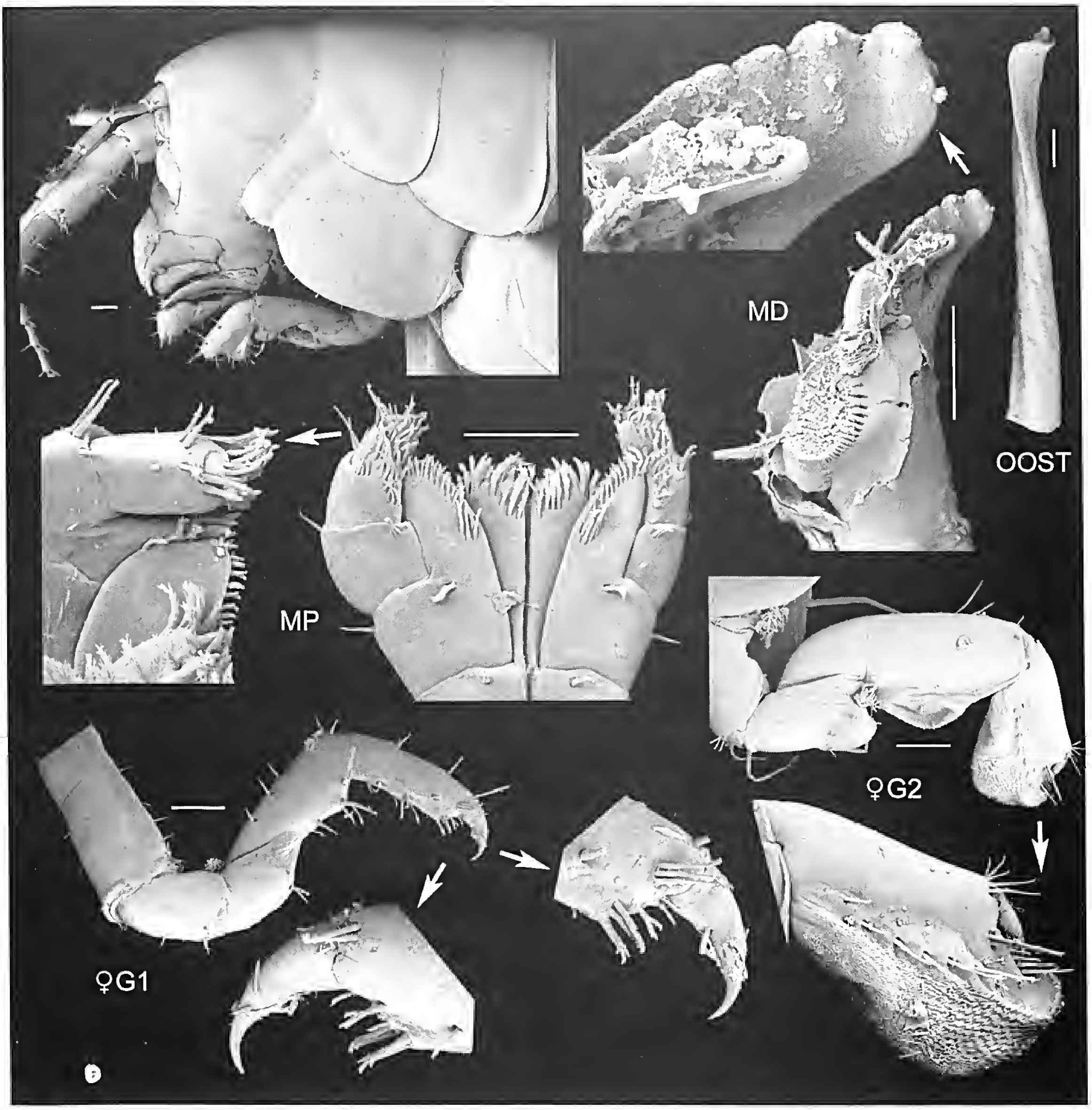

Fig 2. *Floresorchestia australis* sp. nov., holotype, male (NTM Cr.16878), head, paratype, male "b", (NTM Cr.16880), paratype, female (NTM Cr.16879). Scale bars represent 0.1 mm, except oostegite tip represents 0.01 mm.

1 posterior margin of merus, carpus and propodus each without lobe covered in palmate setae; propodus subrectangular; palm acute; dactylus subequal in length to palm. Gnathopod 2 mitten-shaped; coxal gill lobate; basis expanded proximally; ischium without posterodistal lobe on medial surface; posterior margin of merus, carpus and propodus each with lobe covered in palmate setae; carpus well developed (not enclosed by merus and propodus), posterior lobe present, projecting between merus and propodus; palm obtuse, not lined with robust setae, without cuticular patch at corner of palm; dactylus subequal in length to palm. Oostegites setae with spatulate tips. Uropod 1 outer ramus without robust setae.

Habitat. Apparently living on a pebble beach in the supralittoral zone and on the cliff face behind the beach.

Remarks. Only three species of *Floresorchestia* (i.e., *F. australis* from tropical northern Australia, *F. monospina* (Stephensen, 1935) from the Marquesas Islands, and *F. pectenispina* (Bousfield, 1970) from the Solomon Islands) have a large, modified, robust seta on the outer ramus of male uropod 1. Of these species, *F. monospina* has a row of stridulating ridges on epimera 2 and 3 similar to other species in the genus, but *F. australis* and *F. pectenispina* have the stridulating ridges located only on epimeron 2. We think that both of these characters

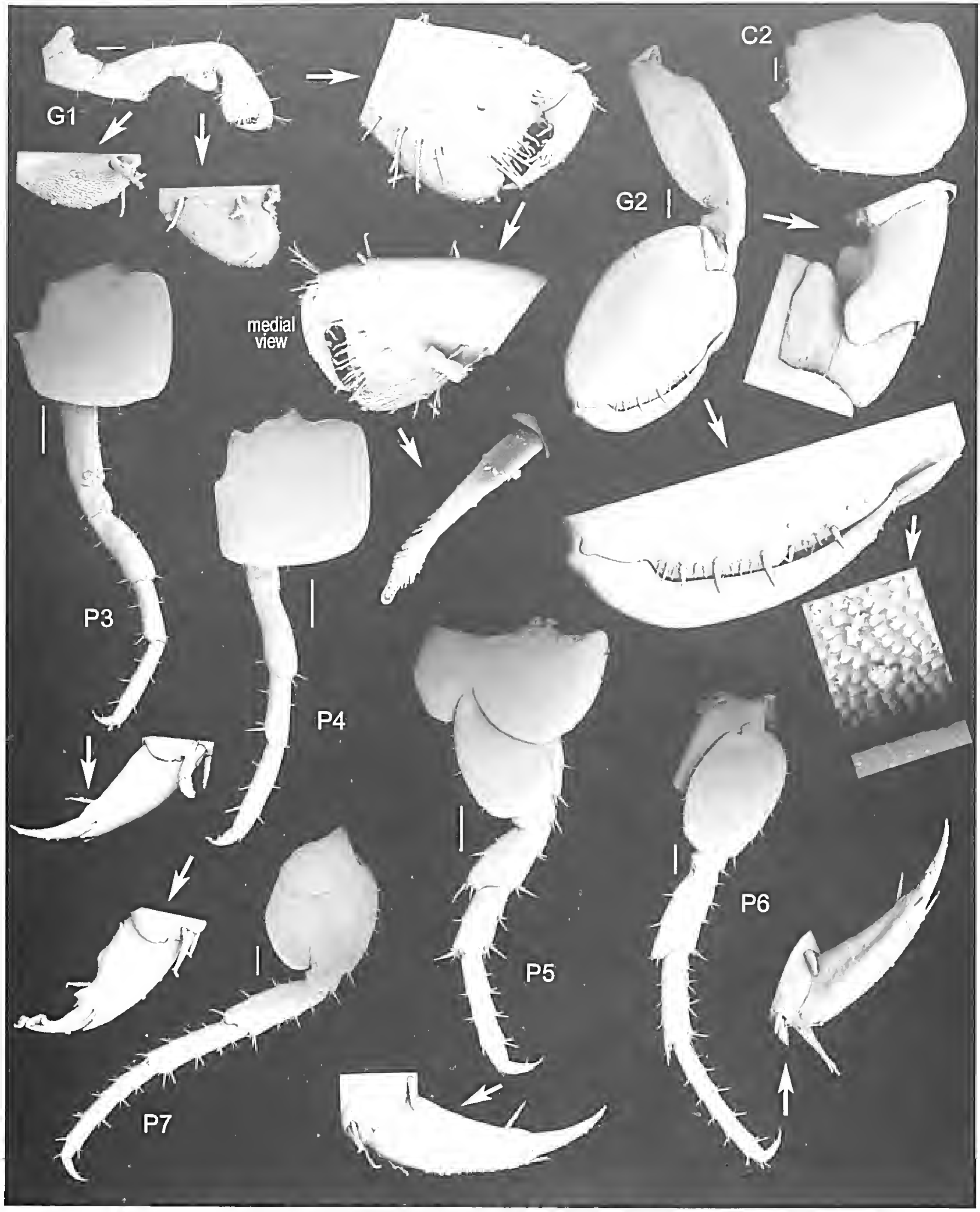

Fig 3. *Floresorchestia australis* sp. nov., holotype, male (NTM Cr.16878). Scale bars represent 0.2 mm.

(the modified robust seta and the stridulating ridges) are powerful synapomorphies indicating sister species status. *Floresorchestia australis* and *F. pectenispina* differ from each other in the shape and structure of the male gnathopod 2, in the setation of uropod 3 and in the depth of the telson cleft.

Distribution. Australia. Northern Territory: Darwin (this study).

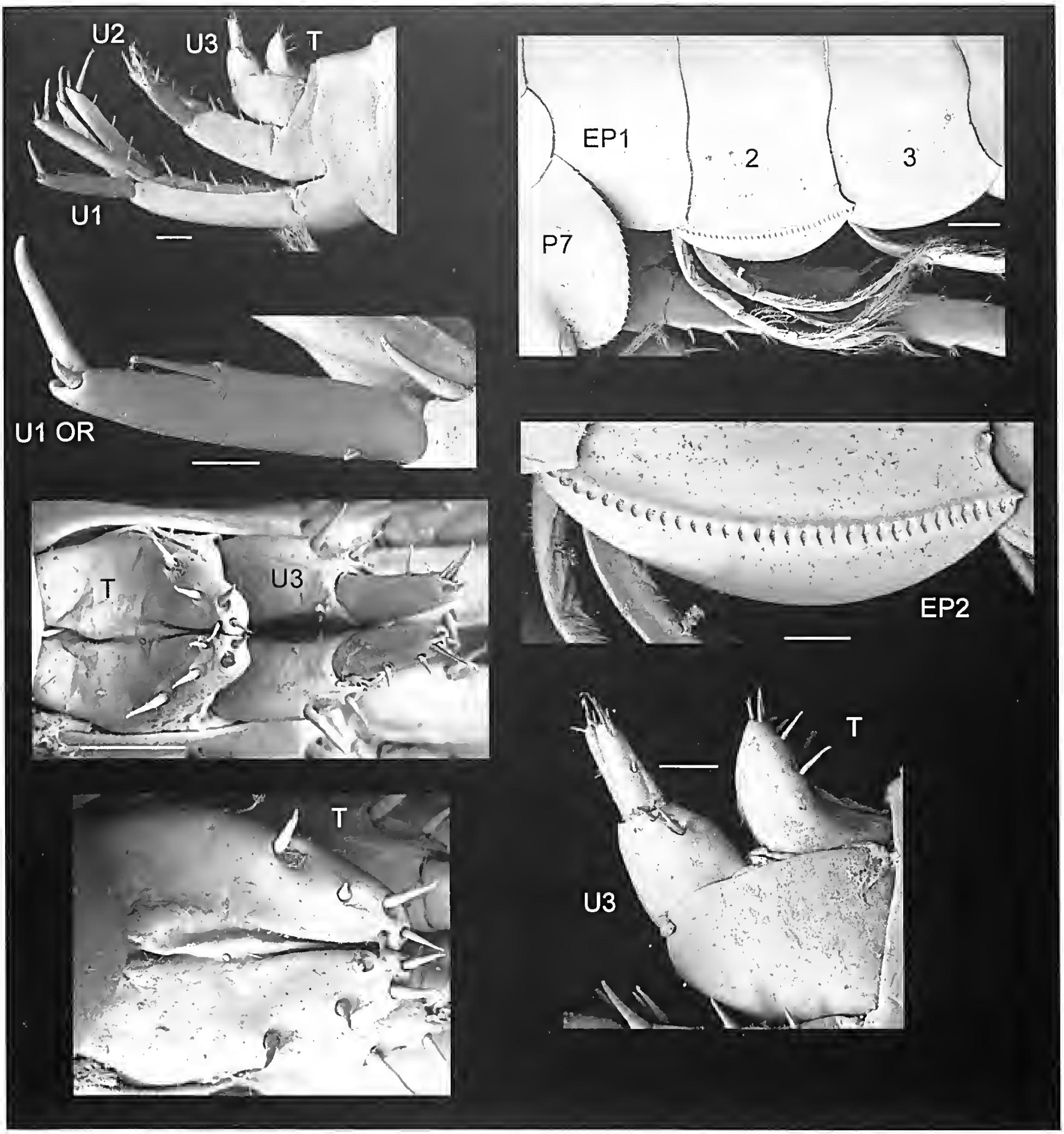

Fig 4. *Floresorchestia australis* sp. nov., paratype, male (NTM Cr.16880). Scale bars for UR, Epimera 1–3 represent 0.2 mm, remainder represent 0.1 mm.

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Description of two new pseudaposematic species with a review of defensive adaptations in the subfamily Thynninae (Hymenoptera: Thynnidae)

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ABSTRACT

Two new species of thynnine wasps, *Lestricothynnus abispoides* and *Zaspilothynnus scolioides*, are described, the males of which are mimics in size and colour pattern of *Abispa* spp. (Hymenoptera: Vespidae) and *Scolia* spp. (Hymenoptera: Scoliidae), respectively. Defensive mechanisms found in the Australian Thynninae are reviewed, including newly discovered defensive pheromones and stridulation.

Keywords. Hymenoptera, Thynninae, *Lestricothynnus*, *Zaspilothynnus*, Australia, pseudaposematic, defence pheromones, stridulation, colour patterns

INTRODUCTION

The Australian Thynninae contains about 600 described species with at least a further 1000 species yet to be described, but present in collections (pers. obs.). Little is known of the biology of the group although they are known to be parasites of scarab larvae (Ridsdill-Smith 1970) and the males of some are specific orchid pollinators (e.g. Bower 1996; Brown 1997a, b; Peakall 1990).

One of the most obvious features of the subfamily is the extreme dimorphism between the sexes. Males are fully winged and are typical wasps in appearance. Females are wingless and somewhat ant-like, but with stouter bodies and the legs partially spinose. This dimorphism has led to a dependence on the males for females to be flown to a food source such as nectar and hemipteran exudates (Given 1954). Strong but flexible coupling mechanisms (Brown 2000) enable pairs to remain in copula for prolonged periods including flight and feeding.

There has been nothing published on the defensive mechanisms within this group, however, as in all Hymenoptera (ants, bees and wasps), it is only the female that can sting using the ovipositor and associated venom glands. The ovipositor's primary function is to lay eggs, but in most Hymenoptera it is also used to paralyse prey or to inject venom as a defensive weapon against larger predators. Males sometimes attempt to "sting" by jabbing a predator with the apex of the abdomen, but males lack both an ovipositor and venom glands.

An examination of museum collections suggests that a number of thynnine wasp species bear a resemblance to paper wasps (Hymenoptera: Vespidae: Polistinae). The females of the latter possess a painful sting. The two Northern Territory thynnines described here are unusual in that their colour patterns are both distinctive within the Australian fauna and that they bear a close resemblance to either potter wasps (Hymenoptera: Vespidae: Eumeninae) or hairy flower wasps (Hymenoptera: Scoliidae).

Other defensive strategies used by males, including stridulation and pheromones, are newly reported and discussed.

Terminology follows Snodgrass (1941), Brown (1997a, b) and Naumann (1991). Relative terms relating to microsculpture are interpreted as follows: sparsely punctate = punctures greater than two puncture-diameters apart; punctate = punctures at most two puncture-diameters apart, but never confluent; closely punctate = punctures almost confluent; rugosely punctate = punctures partially confluent; finely punctate = punctures small and shallow; coarsely punctate = punctures large and deep; obscurely punctate = punctures small, sparse, shallow and only visible at certain angles.

Abbreviations. Morphological characters: T1–7, metasomal tergites 1–7; S1–8, metasomal sternites 1–8. Specimen repositories: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, The Natural History Museum, London (formerly British Museum (Natural History)); NTM, Museum and Art Gallery of the Northern Territory, Darwin (formerly Northern Territory Museum).

SYSTEMATICS

Lestricothynnus Turner, 1910

Type species *Thynnus nubilipennis* Smith, 1879, by original designation. Gender masculine.

Diagnosis. Males are distinguished by antennal prominence broadly rounded (rarely discontinuous

medially), broader than long, and flat (without raised margins) and the body including the metasoma usually extensively coloured; and females by the pygidium oblique, about 4 times longer than wide or longer, longitudinally multicarinate often slightly constricted, never spinose.

Wasps of this genus are medium to small. Typically males are black with yellow or orange markings including paired lateral spots on the abdominal segments and females orange to dark brown without yellow markings.

Remarks. Based on published records, the known distribution is in eastern and southern coastal regions of mainland Australia but discontinuous between north and south Queensland, and between the Eyre Peninsula of South Australia and south-western Western Australia. The genus has not been recorded previously from the Northern Territory.

Lestricothynnus abispoides sp. nov.

(Figs 1–4)

Type material (all Northern Territory). HOLOTYPE – AM, ♂, Stokes Creek, George Gill Range, 26–27 May 1983, G.A. Holloway. PARATYPES – AM, 5♂, same data as holotype; BMNH, 7♂, same data as holotype; NTM I.5374-I.5378, 5♂, same data as holotype; NTM I.5379-I.5380, 2♂, 8 km N of Alice Springs, 8 November 1979, G. Griffin; NTM I.5381, 1♀, Corroborree Rock Conservation Reserve, visiting *Melaleuca bracteata* flowers, 2 December 1993, G.R. Brown; ANIC, 2♂,2♀, Todd River, 23°38'S, 133°53'E, 9 km NbyE of Alice Springs, on flowers of *Prostanthera striatiflora* F. Muell., 28 September 1978, J.C. Cardale; ANIC, 3♂, Entire Creek, 22°58'S, 135°09'E, 155 km NEbyE of Alice Springs, 13 October 1978, J.C. Cardale; NTM I.5382, I.5383, 2♂, Pinnacles Bore 23°14'S, 134°12'E, October 1995, J. O'Grady.

Description of male (Figs 1, 4). Body length 19–22 mm; fore wing 15-16 mm; hind wing 11–12 mm. Clypeus closely punctate; frons, vertex and gena finely and rugosely punctate; occipital and hyperstomal carinae well developed, visible and distinct in profile. Pronotum finely and rugosely punctate to transversely finely and rugosely punctate, anterior margin strongly carinate and produced laterally; mesoscutum rugosely punctate; mesoscutellum rugosely punctate, narrowly sagittally impunctate; metanotum rugosely punctate; propodeum transversely rugosely punctate; mesopleuron plus mesosternum rugosely punctate. Metasoma finely and rugosely punctate, punctures deeper and coarser on apical segments; S1 medially raised; epipygium rounded, transversely multicarinate carinate apically and abruptly produced into large transparent plate; hypopygium triangular with prominent apical spine and basal lobes, dorsal surface weakly transversely carinate. Genitalia: parameres (in profile) broad with ventral margin straight basally and angled ventrally towards apex which is subtriangular with apex rounded, dorsal margin expanded and broadly rounded over most of length, curved longitudinal line of stout bristles on inner surface arising near ventral margin near level of apex of cuspides; digiti large and rounded; cuspides slightly longer than wide, broadly truncate apically, with vertically lamellate longitudinal process arising ventrobasally.

Colour. Mostly orange; mesoscutum, most of mesopleuron except dorsally, mesosternum, T3–4 and S3–4, all black. Wings orange, fore wing with large preapical black spot on costal margin.

Description of female (Figs 2–3). Body length 11 mm. Head subrectangular, wider than long, posterolateral angles broadly rounded; clypeus not sagittally carinate, broadly rounded apically; mandible with fringe of long setae on outer margin ventrally, long, curved, without notches or teeth; frons and vertex almost impunctate; gena sparsely punctate. Pronotum with dorsum subrectangular, wider than long, anterior margin convex, posterior margin weakly concave, impunctate except for a few setiferous punctures at anterolateral angles, setae long; lateral surfaces impunctate. Mesoscutellum impunctate. Propodeum impunctate; lateral margin sharply defined ventrally, less so dorsally; dorsal surface flat, short and wide, wider posteriorly; posterior surface flat and oblique. Metasoma longer than head and mesosoma combined, sparsely punctate on tergites and closely punctate on sternites, segments 2–3 widest; T2 with 6 transverse carinae (including apical and basal), carinae continuous across tergite and not branched; S5 strongly longitudinally carinate, carinae becoming curved outwards posteriorly, closely and coarsely punctate basally. Pygidium (Fig. 3) oblique with lateral margin gradually and slightly converging ventrally, longitudinally multicarinate.

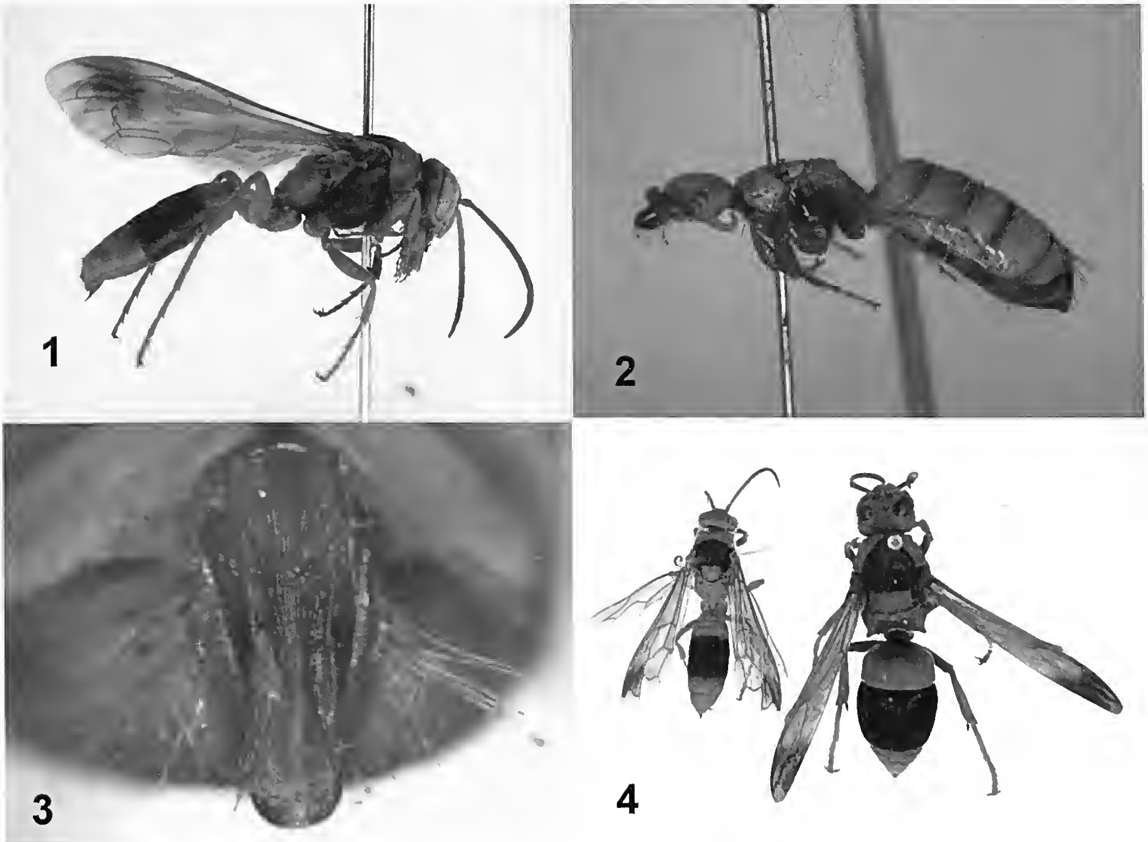
Colour. Mostly yellow: head posteriorly, legs, posterior margin of T1-5 narrowly, pygidium except medially, and sternites, all orange; apex of mandibles, most of mesopleuron and lateral surface of propodeum except dorsal margin and broad medial transverse on pygidium, all brown.

Distribution. Ranges of central Australia in the vicinity of Alice Springs (24°20'S, 131°44'E).

Etymology. The specific name is a reference to a similarity with potter wasps (Vespidae: Eumeninae) of the genus *Abispa* Mitchell (Fig. 4). It is intended as a noun in apposition.

Remarks. This species is not closely related to the type species, *Lestricothynnus nubilipennis* (Smith) which is mostly smooth, polished, and sparsely and shallowly punctate, or any other in the genus. The colour pattern is distinctive and atypical.

The male shows some similarity to *L. constrictus* (Smith) in having a more fusiform metasoma but the latter does not have the epipygium transversely multicarinate. The female differs from *L. constrictus* in that the pygidium is broader dorsally rather than *vice versa*. The sexes were associated by coincident collecting data.



Figs 1–4. *Lestricothynnus abispoides* sp. nov.: **1**, male; **2**, female; **3**, female pygidium; **4**, male (left, mimic) contrasted with *Abispa ephippium* (right, model).

Zaspilothynnus Ashmead, 1903

(Figs 5–12)

Type species *Thynnus leachiellus* Westwood, 1844, by monotypy. Gender masculine.

Diagnosis. Males are distinguished by the combination of posterolateral spines on S6 and the epipygium produced into a subapical plate; and females by an oblique pygidium which is laterally excavate and at least partially transversely or obliquely carinate dorsally but not long and narrow or star-shaped (4-pointed). (Note: it is currently not possible to distinguish this genus from *Leptothynnus* Turner, 1910 or *Pogonothynnus* Turner, 1910, which may or may not be junior synonyms.)

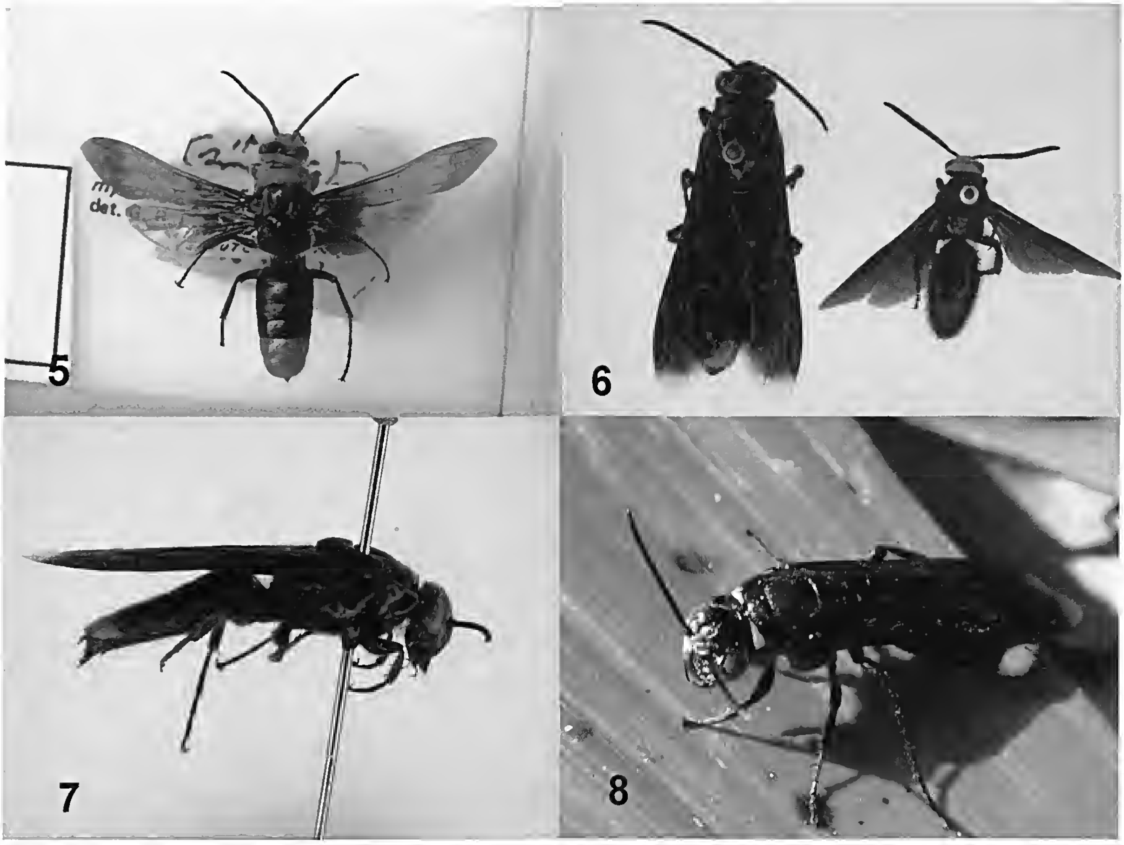
Wasps of this genus are large (body length up to 24 mm). They are usually brightly coloured and many are stout bodied. Less often they are black or mostly so. The Northern Territory species (as well as *Z. cheesmanae* Turner from New Guinea) are rather distinctive in that they have coloured rather than hyaline (or weakly infuscate) wings.

Remarks. This genus is one of the most speciose genera of flower wasps. It contains 37 described species and an unknown number of undescribed species. It is most abundant in eastern and south-western Australia. Four additional species (or subspecies) occur in New Guinea and a single species on Lord Howe Island off the coast of New South Wales (pers. obs.). There are no species recorded from Tasmania and only two previously, *Z. rhynchioides* Turner (Fig. 5) and *Z. ochrocephalus* (Smith), from the Northern Territory.

Zaspilothynnus scolioides sp. nov.

(Figs 6–12)

Type material (all Northern Territory). Holotype – NTM I.5384, ♂, Casuarina Coastal Reserve near Darwin, 12°21´S, 130°52´E, rainforest, 4 October 1997, G.R. Brown. Paratypes – ANIC, 1♂, same data as holotype; BMNH, 1♂, same data as holotype; NTM I.5385-I.5387, 3♂, same data as holotype; QM, 1♂, same data as holotype; WAM, 1♂, same data as holotype; NTM I.5388-I.5399, 12♂, same data as holotype, but dated 24 October 1995; NTM I.53400-I.53407, 8♂, same data as holotype, but dated 5 November 1995; NTM I.5408-I.5411, 4♂, same data as holotype, but dated 12 November 1995; NTM I.4412-I.5417, 6♂, same data as holotype, but dated 19 November 1995; NTM I.5418-I.5419, 2♂, same data as holotype, but dated 14 September 1996; NTM I.5420-I.5427, 8♂, same data as holotype, but

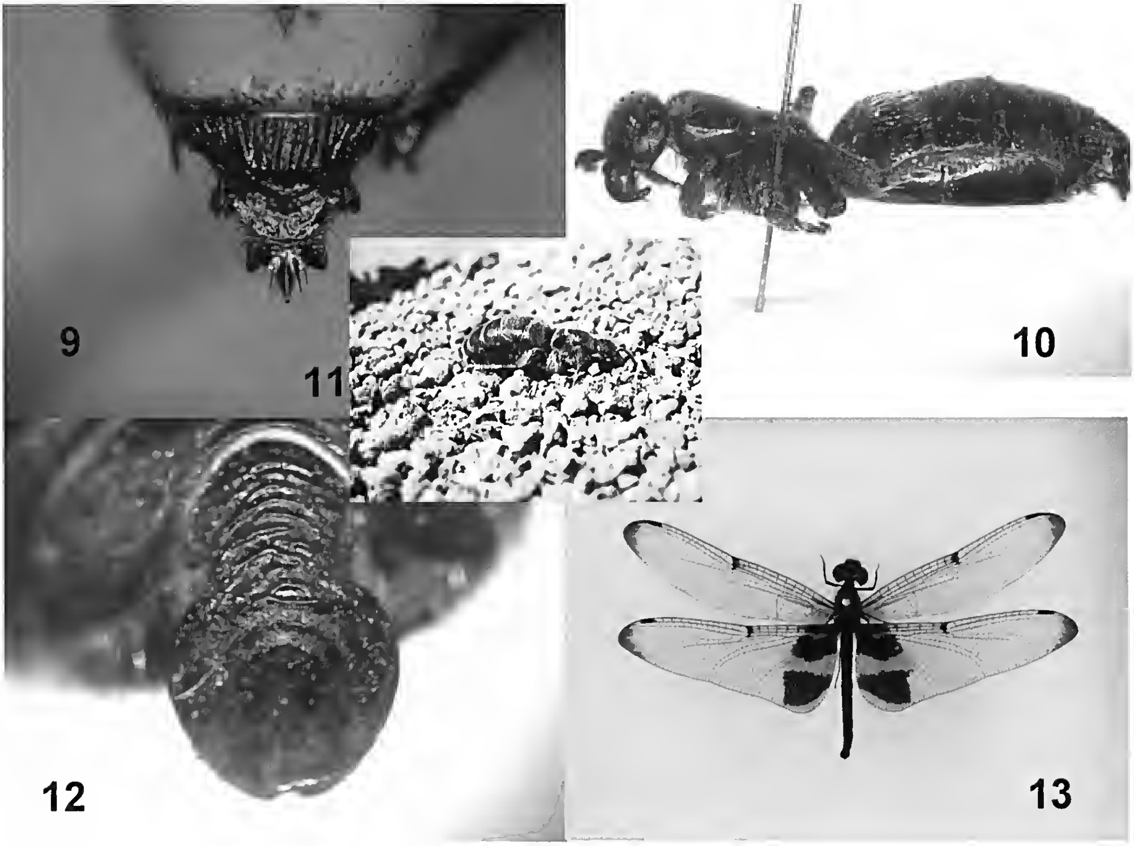


Figs 5-8. Similar-looking wasps showing poseuaposomatic colour patterns: **5**, *Zaspilothynnus rhynchioides*, male; **6**, *Zaspilothynnus scolioides* sp. nov., male (left, mimic) contrasted with *Scolia verticalis* (right, model); **7**, *Zaspilothynnus scolioides* sp. nov., male; **8**, *Zaspilothynnus scolioides* sp. nov., male.

dated 26 October 1996; NTM I.5428, 1♂, same data as holotype, but dated 29 September 1996; NTM I.5429, 1♂, same data as holotype, but dated 18 October 1997; NTM I.5430, 1♂, same data as holotype, but dated 19 October 1997; NTM I.5431-I.5434, 4♂, same data as holotype, but dated October 1997, ANIC, 1♂, same data as holotype, but dated 1 November 1997; BMNH, 1♂, same data as holotype, but dated 1 November 1997; NTM 15435, 1♂, same data as holotype, but dated 1 November 1997; QM, 1♂, same data as holotype, but dated 1 November 1997; WAM 1♂, same data as holotype, but dated 1 November 1997; NTM I.5436-I.5465, 34♂, same data as holotype but dated 8 November 1997, S.M. Gregg; NTM I.5466-I.5476, 11♂, Buffalo Creek, near Darwin, Casuarina Coastal Reserve, sweeping between beach and road, 20 October 1996, G.R. Brown; NTM I.5477, 1♂, Casuarina Beach, 21 October 1991, A. Wells; NTM I.5478, 1♂, Oenpelli, 12°23′S, 133°05′E, November 1996. G.R. Brown.

Additional (non type) material (all Northern Territory): SAM (1♂), Darwin, W.K. Hunt; QM (1♂), Port Darwin, H.W. Brown; SAM (1♂), Groote Eylandt, N.B. Tindale.

Description of male (Figs 6–9). Body length 18–24 mm; fore wing 15–22 mm; hind wing 11–18. Clypeus finely longitudinally striate sparsely overlaid with punctures; frons closely punctate becoming longitudinally rugosely punctate on antennal prominence; vertex almost impunctate; gena closely punctate. Pronotum impunctate, anterior margin with low narrow carina; mesoscutum impunctate except a few scattered punctures anteriorly; mesoscutellum and metanotum sparsely punctate; mesoscutellum sagittally raised and obscurely produced into small knob posteromedially; propodeum with short impunctate dorsal surface and long oblique rugosely punctate surface, lateral surface rugosely punctate; mesopleuron plus mesosternum impunctate becoming finely and closely punctate ventrally and anteriorly. Metasoma with tergites punctate and sternites closely to rugosely punctate; S1 medially raised with a weak posteromedial knob: posterolateral spines on S6 long, digitate and directed posteriorly; epipygium with well defined and strongly longitudinally carinate preapical plate, excavate below this plate and becoming membranous apically; hypopygium 5-spined, basal and lateral spines lobe-like, dorsal surface strongly transversely multicarinate. Genitalia: parameres (in profile) long, narrow and straight, ventral margin curved basally, dorsal margin sharply angled near level of apex of digiti with small notch



Figs 9–13. *Zaspilothynnus scolioides* sp. nov.: **9**, male terminalia, dorsal; **10**, female; **11**, female; **12**, female, pygidium; **13**. *Rhyothemis phyllis*.

basad to this angle, apex rounded, line of stout bristles on ventral margin near apex; digiti small, rounded and visible in profile through small basal notch in paramere; cuspides not reaching to midlength of aedeagus, subtriangular becoming laterally compressed and upturned and almost digitate distally, slightly expanded at apex which visible in profile, ventral margin with long outwardly curged digitate process arising basomedially.

Colour. Black, with inner and outer orbit of eyes narrowly (but broadly interrupted at summit of eye), anterior margin of pronotum broadly, and T5, all yellow. Wings black with iridescent blue reflections, extreme tip of the fore wing hyaline which fully exposes black tip of metasoma. Setae black; white on frons and base of clypeus; brown on anterior surface of tibiae and tarsi. Head, body and appendages, including wings, polished.

Description of female (Figs 10–12). Body length 13 mm. Head subrectangular, wider than long, slightly wider dorsally than ventrally; clypeus sagittally carinate, rounded apically; mandibles long, strongly curved with small notch on inner margin at mid-length; frons deeply punctate, punctures closer on antennal prominence; vertex almost impunctate, becoming closely punctate posteriorly; gena punctate. Pronotum with dorsum subrectangular, wider than long, anterior and posterior margins weakly concave, lateral angles slightly produced, closely and finely punctate becoming less so medially and posteriorly, reticulate; lateral surfaces impunctate and reticulate. Mesoscutellum sparsely punctate. Propodeum with lateral margins sharply defined; dorsal surface flat, short and wide, wider posteriorly, sparsely punctate; posterior surface flat, oblique and very finely punctate dorsally; lateral surfaces polished and impunctate. Metasoma longer than head and mesosoma combined, punctate, punctures deeper on tergites, segments 1–4 the widest; T2 transversely multicarinate, carinae continuous across tergite and becoming finely branched near their lateral extremity; S5 strongly longitudinally carinate, carinae becoming curved outwards posteriorly. Pygidium (Fig. 13) subparallel basally becoming expanded posteriorly into broadly ovate surface that is deflexed and almost vertical; transversely carinate, becoming curved and vertically carinate on dorsal half of posterior ovate surface which is smooth and polished on ventral half.

Colour. Dark brown, almost black.

Distribution. Coastal Northern Territory between Darwin and Groote Eylandt.

Etymology. The specific name is a reference to a similarity with hairy flower wasps (Scoliidae) of the genus *Scolia* Fabricius. It is intended as a noun in apposition.

Remarks. Yellow colouration on pronotum of the male is variable, and may be reduced to large anterolateral spots, or frequently absent. In life and when the wings are closed and at rest, the yellow on T6 is just hidden by the end of the dark colouring of the fore wing, and the hyaline apex of the tip of the fore wing only exposes the black tip of the abdomen to dorsal view.

This new species is closest to *Z. rhynchioides* Turner on the basis of size, the polished body, metasomal shape and the medially raised mesoscutellum. However, the latter species has the metasoma shorter, the head, pronotum and apical three segments of the metasoma uniformly orange, and the wings suffused with orange with the bases and the apex of the fore wing infuscate, and the hypopygium subtriangular with lateral margins emarginate. There is also some resemblance to *Z. ochrocephalus* (Smith), but this is larger and not polished, and has the metasoma uniformly black, conical, and closely punctate rather than polished. The female is not closely related to any other species, although those of *Z. rhynchioides* and *Z. ochrocephalus* are currently unknown

The species described here is easily recognised by its dark blue-black wings like those of scoliid wasps of the genus *Scolia* (Fig. 6).

In Darwin the males are on the wing for a little over two months from late September to early December. The only known female was collected at Casuarina Coastal Reserve in copula and in flight. Separated from the male, it strongly attracted additional males into an open car park well away from the monsoon vine thicket it had inhabited. At another site (Buffalo Creek), it strongly attracted males into a vehicle.

DISCUSSION

Little is recorded about the biology of the Thynninae, and nothing about defensive mechanisms other than a few species being mimics of paper wasps (Vespidae: Polistinae). The distinctive pseudaposematic colour patterns of the two species described here prompts a fuller discussion of mimicry and other presumed defensive mechanisms within the subfamily Thynninae.

Colour. In the Australian thynnine fauna, females are usually uniformly brown, but may range in colour from orange to almost black. Occasionally they are marked with yellow or orange (especially larger species such as those found in *Thynnus* Fabricius and some *Catocheilus* Guérin and *Zaspilothynnus*). This colour pattern is advantageous when females are walking on the surface of the ground and when they are most vulnerable to predators.

The colour patterns of the males are usually more conspicuous and complex. The basic patterns can be grouped as follows:

1. Black with no yellow markings – *Dimorphothynnus* Turner, *Rhagigaster* Guérin, *Rhytidothynnus* Brown and *Umbothynnus* Brown only, however there are some species within the genera *Ariphron* Erichson, *Phymatothynnus* Turner and *Tachyphron* Brown as well as others that are also uniformly black or show slight traces of yellow, especially on the clypeal margin, antennal prominence, pronotal margins and mesoscutellum;

2. Black and extensively marked with yellow including: the margins and much of the disc of the clypeus, antennal prominence, orbits of the eyes, anterior and posterior margins of the pronotum, central mark and lateral line on the mesoscutum, mesoscutellum, disc of metanotum, 2–3 longitudinal marks on propodeum, anterodorsal and anteroventral spots on mesopleuron, margins of mesosternal lamellae, marks on the legs (especially the coxae), paired spots on each tergite and sternite (although reduced in size, or absent, on anterior and posterior segments). The yellow markings are variable within the following extremes: they may be more extensive including enlargement of the metasomal spots are enlarged to form transverse bands or to completely colour the sclerite; or they may be reduced and limited to the margins of the antennal prominence, the anterior margin of the pronotum; and the mesosetellum. Most genera are placed here; and

3. Black with some sclerites mostly yellow or orange (rather than spotted or narrowly margined) – occurs in some *Eirone* Westwood only. However, some species within the genera *Campylothynnus* Turner, *Catocheilus*, *Elidothynnus* Turner, *Macrothynnus* Turner, *Thynnus* and *Zaspilothynnus* have the paired abdominal spots so enlarged and confluent that they form bands on, but unlike *Eirone*, have other markings consistent with group 2.

Apparently independent of the these three basic colour patterns are the colour of the antennae, legs, wings, the presence of brown lateral spots on the vertex and red on the metasoma or mesopleuron. These also appear to be independent of each other (although species with orange antennae often have orange or yellow legs), and are as follows:

a. Antennae brown or orange (usually black) – occurs in some species and is not genera-specific;

b. Black on the legs may be replaced by orange or red (but usually excluding the coxae) – occurs in some species and is not genera-specific;

c. Wings usually hyaline to weakly infuscate, rarely spotted in most *Lestricothynnus* and *Tachynoides* Kimsey and rarely black as in some *Belothynnus* Turner, *Rhagigaster*, *Thynnoides* Guérin, *Thynnus* and *Zaspilothynnus*;

d. Brown lateral spot on vertex – occurs in *Aeolothynnus* Ashmead and some related genera, and is of some generic value;

e. Metasoma red (except bases of T1 and S1) or apical 2 segments red. Occurs in some species of *Dimorphothynnus, Iswaroides* Ashmead, *Lophocheilus* Guérin, *Rhagigaster* and *Zaspilothynnus*; and

f. Mesopleuron uniformly red (usually black, or black with yellow marks, or black replaced with orange) – occurs in some species of *Dimorphothynnus, Rhagigaster* and *Thynnoides*.

Mimicry. A number of species, particularly some species within the genera *Leiothynnus* Turner, *Epactiothynnus* Turner, *Lestricothynnus* and *Zythynnus* Kimsey resemble vespid wasps (Hymenoptera: Vespidae) of the genera *Polistes* Latreille and *Ropalidia* Guérin. Polistine wasps are social, may occur in large numbers, and possess a painful sting. This mimicry is particularly enhanced in *Lestricothynnus* by the presence of a small spot near the pterostigma which occurs in many *Polistes*. This mimicry is most common in eastern Queensland.

Colour pattern 3 possibly mimics potter wasps (Vespidae: Eumeninae) but the resemblance is slight and the two groups are rarely collected at the same time. The colour pattern of *L. abispoides* however, strongly resembles potter wasps especially those of the genus *Abipsa* which are similar-sized and occur widely in Australia including central Australia. The libellulid dragonfly *Rhyothemis phyllis* Lieftinck (Fig. 13), which has black and orange banding the base of the hind wing, also resembles *Abispa* when the dragonfly is flying rapidly to escape a predator.

Black wing colour may mimic that found in the hairy flower wasp genus *Scolia*. *Zaspilothynnus scolioides* strongly resembles this genus of wasps in size, and wing and body colour.

Alarm Pheromones. Insects produce a wide variety of pheromones which serve different functions. Within the Hymenoptera different pheromones are used as sex attractants, trail markers, alarm signals, recruitment to new sites or new food sources, and to stimulate regurgitation in social species (Naumann 1991). These are produced in the mandibular gland and may consist of a mixture of chemicals.

The males of Thynnini, especially the higher Thynnini (referred to as cluster one in Brown (2001)) and including *Lestricothynnus* and *Zaspilothynnus*, produce a pungent odour when handled. This odour is particularly noticeable when specimens are removed from the net by hand, and is present on the fingers after the wasp has been released from the hand. Although the chemical nature is unknown, it is almost certainly defensive and presumably repellent or distasteful. The odour is more distinctive in larger species, but is not strongly offensive to humans. This ocour has not previously been recorded in the Thynninae.

Pseudo-stinging. Only female wasps sting, and some of these can be quite painful. For this reason many serve as models in Batesian mimicry systems (Quicke 1986) with mimics including hoverflies (Syrphidae), soldierflies (Stratiomyidae), robberflies (Asilidae), beeflies (Bombyliidae), clearwing moths (Sesiidae) and longicorn beetles (Cerambycidae), as well as other wasps. This includes the two new species described here.

While Batesian mimicry is most frequently seen in the form of similarities in colour, it can be behavioural in the form of a pseudo-sting, or pseudo-stinging behaviour.

The pseudo-stinging apparatus resembles the ovipositor of a female wasp. It may be in the form of pointed parameres or other parts of the male genitalial capsule, or other pointed processes that vary between taxa. In male Scoliidae the hypopygium (subgenital plate) has three long apical spines, while those in Thynnidae vary from none to five spines (Fig. 9).

Pseudo-stinging is a behaviour in which male wasps attempt to sting, even though there is no stinging mechanism present. This behaviour is strong in male scoliids when they are handled, and in larger specimens the apical spines do occasionally pierce the skin. In thynnids this behaviour may also be vigorous especially in larger specimens, but the spines are smaller and blunter, and cannot pierce the skin (although the mandibles sometimes can do so in larger species). Although many thynnids have weak or occasionally no spines, they all use this pseudo-stinging behaviour.

Stridulation. Stridulation and other forms of sound production are well known within the order Hymenoptera (Naumann, 1991). This includes rubbing wings against roughened lobes (cenchri) on the metanotum in some sawflies (Pergidae), a loud buzzing by some bees (Apidae), mud daubers (Sphecidae) and potter wasps (Vespidae: Eumeninae), and stridulation in some ants (Formicidae) and velvet ants (Mutillidae). However, little is known about why insects produce sound. It has been suggested that loud buzzing by mud daubers during mud collection helps to compact the mud. However, it could also be a deterrent to predators as similar sounds are produced in other groups such as bees which do not collect mud.

Ants, which have a complex social structure, use a variety of communication systems including chemical, visual and tactile methods, as well as drumming and stridulation. The latter is produced by raising the gaster causing a file on the third metasomal segment to rub against a plectrum on the second segment. These structures are usually located dorsally (Hölldobler and Wilson 1990).

A similar stridulatory mechanism occurs in velvet ants between the second and third metasomal segments, but on the ventral surface. Stridulation occurs in both sexes during mating and when individuals are disturbed (Manley 2000).

Males of the Australian genera *Dimorphothynnus, Eirone, Rhagigaster, Rhytidothynnus* and *Umbothynnus* (Rhagigasterini) stridulate when they are held with the fingers. This sound is audible and is produced by extending and contracting the metasoma. A dissection of males has not revealed any specialised internal structures on the sclerites, but sound can be generated in freshly killed specimens by

moving the metasoma in and out manually with the hands. This may be similar to that reported in mutillids (Manley 2000), but I can find no evidence of a basal file on T3 as in mutillids or on any other metasomal sclerite. This sound is a squeaking noise with a frequency of about two cycles per second.

It is not known if stridulation occurs in the Neotropical rhagigasterine genus *Aelurus*, but it does not occur in any other genus I have collected, and it does not occur in the females.

Sound production is probably defensive in thynnines as it has only been observed when wasps are held by the mesosoma by the fingers.

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A new species of *Clavisyllis* Knox, 1957 (Polychaeta: Syllidae): a genus with the unusual distribution of New Zealand and the Great Barrier Reef, northern Queensland, Australia

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ABSTRACT

An intriguing small syllid polychaete belonging to the genus *Clavisyllis* Knox, 1957 is described from coral reefs of northern Queensland, Australia. *Clavisyllis yongei* sp. nov. possesses large inflated lobe-like dorsal cirri, coloured yellow-orange with white tips, that alternate in segmental insertion positions and form longitudinal rows down the dorsum; similar shaped dorsal tentacular and antennal cirri, large nuchal epaulettes, elongate palps fused only at their base, and a pharynx with a trepan. The new taxon is compared with the only other species in the genus *Clavisyllis alternata* Knox, 1957, and possible scenarios for the unusual geographic distribution of tropical northern Australia and temperate New Zealand are discussed. *Clavisyllis* is also compared with *Eurysyllis*, another syllid genus possessing rows of dorsal lobes, specifically *Eurysyllis japonica* Imajima, 2003, a new record for the Great Barrier Reef, Australia.

KEYWORDS: Annelida, Polychaeta, Syllidae, *Clavisyllis yongei* sp. nov., *Clavisyllis alternata, Eurysyllis japonica*, taxonomy, systematics, coral reefs, biogeography.

INTRODUCTION

The family Syllidae, known to be especially abundant in shallow waters, is one of the most diverse polychaete families comprising 70 genera (Aguado and San Martín 2009). There have been a number of recent papers revising the Australian syllid fauna by subfamily: Exogoninae (San Martín 2005), Eusyllinae (San Martín and Hutchings 2006) and Syllinae (San Martín *et al.* 2008a,b) which have substantially increased our knowledge of the syllid fauna with the addition of a number of new genera and species plus a better understanding of the phylogeny of the group (Aguado and San Martín 2009).

The monotypic syllid genus *Clavisyllis* was originally described from an individual that was living on hydroids of the genus *Sertularia* by Knox (1957) from Banks Peninsula, South Island, New Zealand. The holotype was subsequently lost, although Aguado and San Martín (2008) redescribed *Clavisyllis alternata* from another single specimen taken on a pier at the port of New Plymouth, North Island, New Zealand. All these previous authors have remarked on the number of morphological features that did not relate to any existing syllid generic or subfamilial designation.

Two syllid individuals, recently collected from Lizard Island, Great Barrier Reef, northern Queensland, with large ovoid lobes superficially appearing to be in two longitudinal rows down the dorsum, were originally compared with those seen in *Eurysyllis*. Aguado (pers. comm., September 2009) alerted the author to the existence of the genus *Clavisyllis* and after re-examination of the literature and the Great Barrier Reef (GBR) specimens, these ovoid lobes were found to be modified dorsal cirri that subtly alternate in segmental position along the body, a primary feature of *Clavisyllis*. The GBR material possesses different morphology of the ventral tentacular cirri, nuchal epaulettes, pharynx and numbers of neurosetae in comparison to *Clavisyllis alternata* and is described herein as a new species.

Material from Lizard Island was collected under the auspices of the CReefs project organised by the Australian Institute of Marine Science (AIMS). Type and non-type material is deposited in the Museum and Art Gallery Northern Territory, Darwin (NTM) and the Queensland Museum, Brisbane (QM).

SYSTEMATICS

Family Syllidae Grube, 1850
Subfamily uncertain
Clavisyllis Knox, 1957

Gender feminine. Type species, by monotypy, *Clavisyllis alternata* Knox, 1957. Recent, New Zealand.

Diagnosis. Subcylindrical broad body with crowded large ovoid dorsal cirri, subtly alternating in lateral and dorsal segmental position giving the appearance of 4 longitudinal rows of lobes down body; integument thin. Prostomium with 4 eyes, 3 antennae and 2 palps fused at base. Nuchal organs form 2 straight epaulettes with single digitiform nuchal cirrus (*Clavisyllis alternata)* or curved

epaulettes with knob-like tips (*Clavisyllis yongei* sp. nov.) along posterior edge of prostomium.

Peristomium with 2 pairs of tentacular cirri. Antennae, dorsal tentacular cirri and dorsal cirri large, ovoid, inflated, with cirrophores; ventral cirri triangular. Parapodia uniramous with projecting upper lobe, 1–2 aciculae and compound heterogomph falcigers with blades having distinct bidentate tips and long spines forming aristae distally. Pygidium with 2 short ovoid cirri. Pharynx with single tooth or trepan of 12–13 teeth.

Remarks. Neither Knox (1957), nor Aguado and San Martín (2008), nor the present author can assign this genus to any subfamily of the Syllidae.

The presence/absence of ventral cirri, the degree of articulation of the antennae and cirri, the degree of fusion of palps, the shape of nuchal organs, and most importantly the method of reproduction, are among the major traditional criteria used to define position of syllid genera within a subfamily (Garwood 1991; Glasby 2000; Aguado and San Martín 2009). *Clavisyllis* has, for example, unarticulated cirri, partially fused palps, nuchal epaulettes, two pairs of tentacular cirri and a pharynx with either a single tooth or trepan, characters that overlap across genera in a number of syllid subfamilies.

Certain *Clavisyllis* features are seen in some genera of the Autolytinae such as the large nuchal epaulettes present in *Proceraea aurantiaca* and the large lobe-like antennae in *Paraprocerastea draculai* (San Martín 2003). However, the Autolytinae possess a coiled pharynx and no ventral cirri; *Clavisyllis* has a straight pharynx and ventral cirri.

The genus has basally fused palps and unarticulated cirri that are indicated for the Eusyllinae. Aguado and San Martín (2008) consider that *Clavisyllis* also has some common features with *Amblyosyllis* (currently located in the Eusyllinae) such as the presence of extended parapodial lobes and nuchal epaulettes.

Clavisyllis shares with *Eurysyllis* (currently located in the Syllinae due to its schizogamic reproduction) large lobe-like antennae, tentacular cirri and unarticulated dorsal cirri. The smooth inflated cirri seen in both genera, plus the additional rows of dorsal lobes present in *Eurysyllis*, may represent characters modified from a more typical form of syllid ancestor for some specific camouflage or mimicking advantage. These modifications make placement within a subfamily difficult and in the case of *Clavisyllis* impossible until more material is collected and reproduction method observed.

Clavisyllis yongei sp. nov.

(Figs 1–3)

Material examined. Holotype – Australia, Queensland, Great Barrier Reef, Yonge Reef, 14°36′S, 145°37′E, Stn. CWLI040, coarse coral rubble, 30 m, coll. S. Smith and J. Caley, 21 February 2009, NTM W.22995; Paratype – same collection details as holotype, 1, NTM W.22994.

Description. Holotype entire body 5.1 mm long, 1.5 mm wide, 51 segments. Paratype, body 5.0 mm long, 1.72 mm wide, 49 segments.

Description based on holotype except where indicated otherwise. Living colour orange-yellow, body broad, elongated, dorsally arched, largely covered in distinctive inflated yellow-orange ovoid lobes with peaked distal white tips (Fig. 1); small uniramous parapodia tucked under, not visible dorsally, ventrum flat.

Prostomium about twice as wide as long with 2 pairs of large, lensed, red eyes; large lobe-like median antenna arising from posterior half of prostomium; 2 smaller lateral antennae inserting near anterior edge of prostomium; 2 palps with wide base and subulate tips, fused only at basal quarter of length, inserting ventrally. Nuchal organs form 2 prominent curved epaulettes along posterior edge of prostomium (seen clearly with white margin under stereo microscope) with elevated knobs at ends (Fig. 2A,B). Pharynx straight, similar length or longer than proventricle, with trepan of 12–13 teeth including 1 slightly longer mid-dorsal tooth at ventral anterior pharyngeal border; proventricle cylindrical to ovoid, from setiger 8–9 with about 40 rows of muscle cells and distinct midline (paratype, Fig. 3A,B).

Peristomium very reduced, not visible dorsally, asetose, with 2 pairs of tentacular cirri; dorsal pair ovoid, ventral pair cylindrical inserting next to palps (Fig. 2B). Chaetiger 1 and following chaetigers with uniramous parapodia with large ovoid dorsal cirri alternating in their point of insertion; dorsal cirri more dorsally inserted approximately same size as those inserted more laterally. Parapodia with distinct projecting upper lobe (almost cirrus-like) and larger triangular/ovoid-shaped ventral cirri, both extending beyond tips of parapodium; 2 aciculae (superior excavate on lower edge, inferior entire); compound chaetae heterogomph falcigers with mostly smooth shafts (see some with minute serration) and medium-short, smooth, falcate blades with distinct bidentate tips and long pointed single or multiple spines forming aristae distally (Figs 2C, 3D–H). Numbers of chaetae similar down body, 6–8. Dorsal chaetae absent. Single simple chaetae only present in posteriormost 2–3 segments, very slender with slight curve. Pygidium with 2 short ovoid cirri (Fig. 3C).

Remarks. Live *Clavisyllis yongei* resembled a small nudibranch when first seen in the field (Fig. 1) with the upright dorsal cirri lobes very similar in appearance to the erect cerata held over the dorsum in a number of families of aeolid nudibranchs. Among the often very colourful aeolid nudibranchs, for example, basally swollen cerata with elongate tips are arranged in simple rows down the back and in many species have white distal tips which are usually where the cnidosacs for nematocyst storage are situated. As well as the bright colouring advertising its possible toxicity to predators, the aeolid body form often mimics the structure and colour of its food source, e.g. soft corals or hydroids (Debelius and Kuiter 2007).

Fig.1. *Clavisyllis yongei* sp. nov. Live, paratype (NTM W.22994), lateral view, 5 mm body length. Photo. Art Anchor.

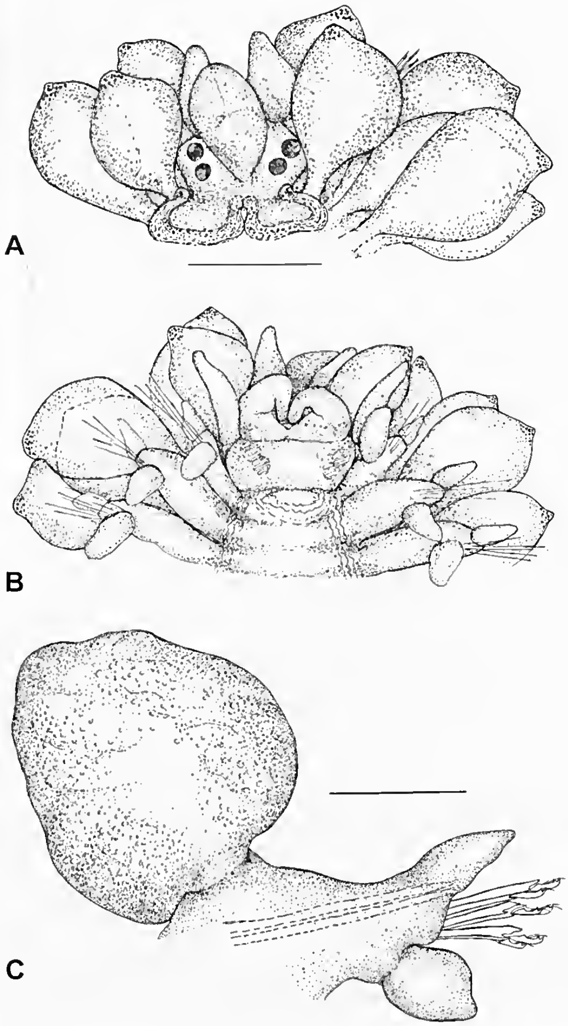

Fig. 2. *Clavisyllis yongei* sp. nov. Holotype (NTM W.22995), **A**, Anterior end, dorsal view, scale bar 0.2 mm; **B**, ventral view, same scale as Fig. 2A; **C**, mid body parapodium, scale bar 0.1 mm.

Among the polychaetes, the Syllidae are relatively commonly associated with other marine invertebrates as commensals on the surface of the host and may mimic its bright colour and structure, e.g. *Alcyonosyllis phili* Glasby and Watson, 2001 associated with a nephtheid soft coral from Darwin Harbour and *Alcyonosyllis glasbyi* San Martín and Nishi, 2003 associated with a gorgonian from Japan. It is possible the body form and colouration of *Clavisyllis yongei* may confer some advantage in mimicking either a nudibranch species or a possible invertebrate host. The two *C. yongei* specimens collected came from coral rubble washings with some encrusting algae, but in the absence of specific nudibranch comparative material or more detailed microhabitat information this must remain speculation.

The single existing specimen of *Clavisyllis alternata*, prepared for SEM, was not examined for this study as both Knox (1957) and Aguado and San Martín (2008) have provided well documented and illustrated papers. It is clear to this author that *C. yongei* from the GBR, northeastern Australia, and *C. alternata* from New Zealand are taxa belonging to the same genus. Both species have similar features of the anterior end including possession of large epaulettes, alternating ovoid dorsal cirri lobes down the dorsum and unusual falcigerous blade details. The orange-yellow colouration of the two species in life is also the same (see *C. alternata*, Knox 1957: 493).

The major difference between the two species is the shape of the nuchal organs, which form two curved connected epaulettes in *Clavisyllis yongei* and two straight unconnected epaulettes in *C. alternata*. The latter also has a single digitiform nuchal cirrus, unique among the entire Syllidae, which is lacking in *C. yongei*, although the ends of its epaulettes are elevated slightly into raised knobs. While the shape of the pharynx and proventricle are very similar between the two species, *C. yongei* possesses a trepan of many teeth and *C. alternata* possesses a single tooth.

Clavisyllis yongei also has a distinctly different shaped ventral tentacular cirri pair, a larger projecting upper parapodial lobe and smaller number of falcigers (6–8 versus 30).The GBR specimens are shorter (5 mm versus 13–29 mm in length in the NZ specimens). There is a different proportion of the supra-acicular parapodial lobes to the parapodium between the species and the GBR specimens and also a glandular (versus reticulate) pattern of the dorsal cirri (Fig. 2C this paper, as compared with Aguado and San Martín 2008: 45, fig. 6c).

The characters separating the two species are of interest, being a mixture of what is commonly thought of as characters at the generic level e.g. nuchal epaulette shape, pharnyx details, tentacular cirri shape, as well as the

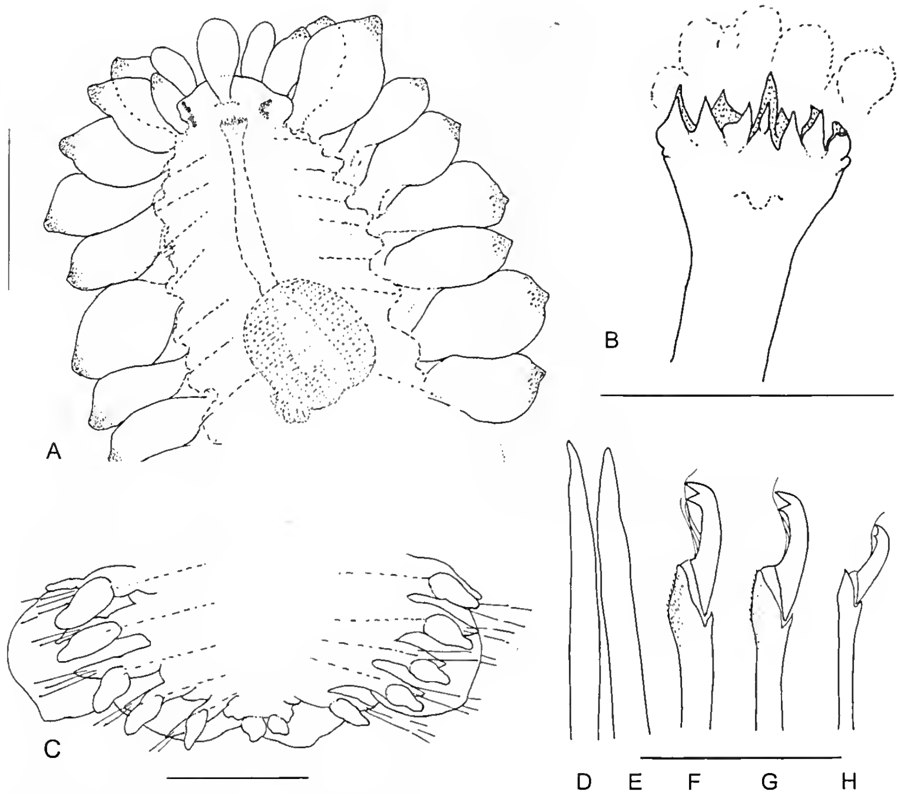

Fig. 3. *Clavisyllis yongei* sp. nov. Paratype (NTM W022994), **A**, anterior end, dorsal view, scale bar 0.2 mm; **B**, detail of trepan, scale bar 0.1mm. Note: dorsal lobes flattened laterally due to coverslip. Holotype, **C**, posterior end, ventral view, scale bar 0.2 mm, **D**, **E**, aciculae, **F**, **G**, midbody falcigers, **H**, posterior falciger, scale bar 0.04 mm.

more conventional species level characters e.g. numbers of chaetae, parapodial lobe shape, epidermal texture.

This discrepancy in shared *Clavisyllis* characters may well be evidence of a former ancestral population being separated for a long time. In a checklist of New Zealand Annelida (Glasby *et al.*, 2009), *Clavisyllis* is cited as an endemic genus, a situation now changed with the discovery of this new species from the Great Barrier Reef, north-eastern Australia.

Glasby and Alvarez (1999) found that the polychaete fauna of New Zealand was overwhelmingly of southern or Gondwanan origin with over half of all polychaetes endemic to New Zealand or shared with southern Australia. The same conclusions have been voiced by R. Willan for the Mollusca (pers. comm.) and T. O'Hara for the ophiuroids (pers. comm.).

Glasby and Alvarez's (1999) suggestion that the Greater New Zealand region is 'monophyletic' with respect to polychaetes (i.e. comprising a genuine biogeographical entity), implies that the fauna evolved after the separation of New Zealand from Gondwana. Taxa that evolved before the separation of New Zealand from Gondwana would potentially show present day distributions that included other Gondwanan lands such as Australia. New Caledonia also formed part of the edge of Gondwana with New Zealand for part of the Cretaceous (Heads 2009).

Heads (2009) also emphasises that parts of New Zealand, New Caledonia, New Guinea and the Bismarcks/Solomons are derived from ancient Central Pacific rifted terranes that were never part of Gondwana.

Clavisyllis, an enigmatic and rare genus, is presently known only from New Zealand and north-eastern Australia. It is possibly a very old taxon allied either to the edge of Gondwana, pre-dating the Australia/New Zealand split, or from rifted oceanic terranes derived from island arcs of the ancient Central Pacific.

There is also the consideration that the existence of a relatively shallow water connection between eastern Australia and New Zealand enabled dispersal of *Clavisyllis* at some time in the more recent past along shallow water bridges and interconnecting islands. Potential connection is offered, for example, by the Lord Howe Island Rise, a continental fragment extending northwards from the Challenger Plateau off the west coast of New Zealand, which remained very close to Australia until the Middle Tertiary (Walley 1992). While nothing is known of the reproductive strategies or larval stages of *Clavisyllis* it seems an unlikely proposition that dispersal could be taking place

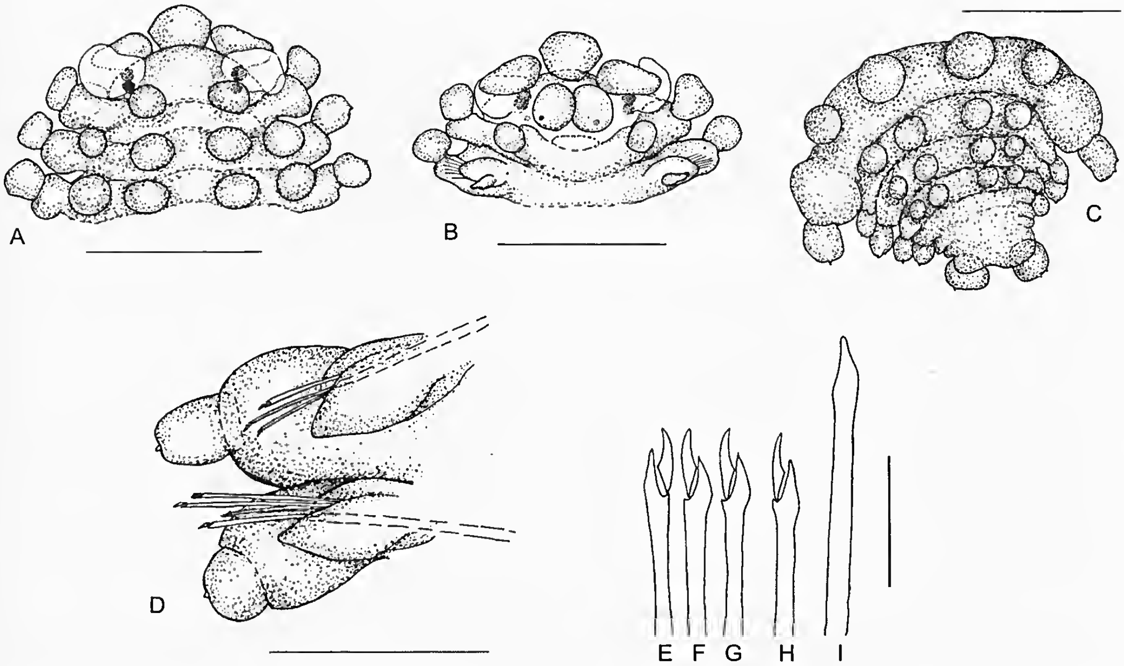

Fig. 4. *Eurysyllis japonica* (NTM W.22996), **A**, Anterior end, dorsal view, scale bar 0.2 mm; **B**, ventral view, scale bar 0.2 mm; **C**, posterior end, dorsal view, scale bar 0.2 mm; **D**, mid body parapodium, scale bar 0.1 mm; **E-G**, midbody falcigers; **H**, posterior falciger; **I**, acicula, scale bar 0.01 mm.

over the present deep water barriers between Australia and New Zealand.

Habitat and Distribution. Presently only found from coral rubble at 30 m depth, Great Barrier Reef, northern Queensland.

Etymology The species is named *yongei* after Charles Maurice Yonge, eminent marine biologist and leader of the Great Barrier Reef Expedition of 1928–29. His name was given to Yonge Reef on the Outer Great Barrier Reef from where *Clavisyllis yongei* was discovered.

Subfamily Syllinae
Eurysyllis Ehlers, 1864

Gender feminine. Type species, by monotypy, *Eurysyllis tuberculata* Ehlers, 1864. Recent, Mediterranean Sea.

Eurysyllis japonica Imajima, 2003
(Fig. 4)

Material Examined. Australia, north Queensland, Great Barrier Reef, Day Reef, 14°28′S, 145°32′E, Stn. CWLI038A, coarse coral rubble, 19 m, 19 February 2009, coll. N. Bruce, 1, NTM W.22996; Linnet Reef, 14°46′S, 145°20′E, Stn. CWL1027, coarse coral rubble, 2–12 m, 23 February, coll. P. Bock, 1, QMG231603; Yonge Reef, 14°36′S, 145°37′E, Stn. CW L1040, coarse coral rubble, 30 m, 21 February 2009, coll. K. Mills, 1, NTM W.22997.

Description. Based on largest specimen from Day Reef, 5.0 mm long, 0.8 mm wide, 89 segments; body entire. Colour in life whitish grey, 'crusty' looking. Body elongate, ribbon-like, slightly convex anteriorly, with 4 flattened rounded tubercles per segment (2 on peristomium), forming 4 longitudinal rows down body (Fig. 4A,C).

Prostomium about twice as wide as long, with 2 pairs of red eyes dorsally and 1 tiny pair visible ventrally near palps. Three spherical antennae, 2 lateral, 1 median, on anterior edge of prostomium plus 2 dorsolateral lobes arising from lateral edge of prostomium over anterior pair of eyes. Two spherical palps ventrally positioned, fused along their length (Fig. 4 A–C). Nuchal organs not observed. Pharynx slender, long, no tooth observed; barrel-shaped proventricle through segments 19–22, with about 14 muscle cell rows.

Peristomium with 2 dorsal tubercules and 2 pairs of tentacular cirri; dorsal pair same shape as subsequent dorsal cirri, ventral pair short and rounded only visible ventrally. Segments numerous and short; dorsal cirrophores well developed with ovate cirrostyles with 1–3 minute papillae distally; ventral cirri triangular (Fig. 4D). Compound chaetae of mid-body segments heterogomph falcigers, shafts smooth, articles short, smooth, very small; single acicula with projecting tip (Fig. 4E–I). Numbers of falcigers similar down body, numbering 6–8, with single simple chaeta present in posterior segments. Pygidium with 2 ovate anal cirri, similar to dorsal cirri (Fig. 4C).

Remarks. *Clavisyllis* bears a superficial resemblance to *Eurysyllis*, particularly in the apparent possession of the four longitudinal rows of rounded lobes down the dorsum, a character only truly occurring in *Eurysyllis.* Both genera also fall into a similar size range and interestingly both were present in the same Great Barrier Reef habitat.

There are four *Eurysyllis* species reported – *E. tuberculata* Ehlers, 1864, *E. pacifica* (Hartman, 1954), *E. spicum* Kudenov and Harris, 1995, and *E. japonica* Imajima, 2003. Specimens examined from three GBR reefs, northern Queensland, possess tiny papilla/e on the cirrostyles, smooth short falcigers, and a slender acicula with a pointed end (Fig. 4), features observed in, and unique to, specimens of *Eurysyllis japonica*. This is therefore the first record of this species occurring within Australia.

San Martín *et al.* (2008a) figured and described *Eurysyllis tuberculata* as occurring widely in Australia, from mainly southern temperate waters and northwestern Western Australia. *Eurysyllis tuberculata* differs from *E. japonica* in having non-papillate cirri, falcigers with spinose shafts and articles and a distally expanded tip of the aciculae.

Eurysyllis is placed in the Syllinae, a subfamily characterised by articulated appendages, free or partially fused palps and undergoing schizogamic scissiparous reproduction. From my observations, *Eurysyllis japonica* has smooth antennae, tentacular cirri and dorsal cirri, fused palps and non-alternating anterior end dorsal cirri (but see Character matrix, Table 3, Aguado and San Martín 2009). The dorso-lateral lobes of the prostomium of *Eurysyllis* appear to be a unique character of the genus, but it is not included in the Character states, Table 2, Aguado and San Martín 2009.

Habitat and Distribution. Recorded from coral rubble at 2-30 m depth, Great Barrier Reef, north Queensland.

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POSTSCRIPT

A further single specimen of *Clavisyllis yongei* was collected on 14 November 2009 at 30 m, from Sykes Reef, Capricorn Group, southern Great Barrier Reef, central Queensland (23°26´S, 152°02´E), during the recent CReefs sampling expedition to Heron Island.

The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 2009 **25**: 87–102

Description of four new species of limestone-associated *Torresitrachia* land snails (Mollusca: Pulmonata: Camaenidae) from the Katherine District of the Northern Territory, Australia, with comments on their conservation

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ABSTRACT

Four new species of land snails of the genus *Torresitrachia* (Pulmonata: Camaenidae) are described from the Northern Territory of Australia: *T. darwini, T. wallacei, T. cuttacutta, T. alenae.* The species are distinguished on the basis of differences in shell and animal morphology, and 16S DNA analysis. All four species occur in the Katherine District (Daly Basin Bioregion), and have remarkably small geographical ranges and fragmented populations. Though not all species of *Torresitrachia* are associates of limestone, these four species are obligately associated with limestone outcrops supporting monsoon/deciduous vine thicket vegetation. Annual grasses, which are replacing the natural vegetation, do not offer suitable habitat for these land snails and they are much more prone to the 'grass/fire cycle', thus threatening the snails' long term survival. Presently all the known populations of two of these new snails, *T. wallacei* and *T. alenae*, appear to be under threat of extinction and none occurs within any reserve.

Keywords: Mollusca, Pulmonata, Camaenidae, *Torresitrachia*, new species, Australia, Katherine, limestone outcrops, taxonomy, habitat fragmentation, conservation.

INTRODUCTION

Charles Darwin (1856) realised that land snails make excellent subjects for biogeographic analyses because of their limited powers of dispersal. His views were succinctly summarised by Örstan and Dillon (2009) who said: "Darwin's central thesis, that all organisms have diverged from common ancestors, required that they originate at single points, and disperse throughout the world. So if a convincing case could be built for land snails, surely to be ranked amongst the most disadvantaged of the world's dispersers, perhaps the remainder of the worldwide biota might fall into line."

Land snails do make good subjects for biogeographic studies, but unfortunately their populations are also very prone to fragmentation, leading to decline and often extinction of the species. Of all the major groups of invertebrates, the largest number of documented extinctions has occurred amongst the non-marine molluscs (Groombridge 1994). The extent of change to natural habitats right across the 'wet-dry' tropics of the north of the Australian continent has increased dramatically since European settlement almost certainly leading to substantial declines in abundance of endemic land snails. Already 31 species of land snails are listed as threatened by habitat loss in the Northern Territory, of which eight occur in the 'wet-dry' tropics (Woinarski *et al.* 2007). Thirty of these snails belong to the Camaenidae, but none of them is in the genus *Torresitrachia*.

Here we describe four new species of *Torresitrachia* occurring in the Katherine District (Daly Basin Bioregion as defined by Thackway and Cresswell (2005)) and restricted to limestone outcrops of the Tindall Limestone Formation where they have very small geographic ranges. Observations by one of us (Vince Kessner) spanning thirty years, plus our own quantitative surveys, have shown these habitats associated with the limestone outcrops are threatened by changed fire regimes with seasonal grasses replacing the closed monsoonal vine-thicket forest (*sensu* Wilson *et al.* 1990) with concomitant loss of leaf litter and increasing aridity of the soils (Braby *et al.* In prep.).

MATERIAL AND METHODS

The conchological separation of the four *Torresitrachia* species described here were made by comparisons between large numbers of specimens (numbers are given at the start of the Description for each species) jointly by Willan, Kessner and Köhler based on shell morphology and location. Köhler dissected two or three specimens of each species for the anatomical account and prepared the illustrations.

Table 1. List of sequenced samples of Camaenidae material (in addition to the four new species of *Torresitrachia* described herein) to construct the phylogenetic tree shown in Fig. 15.

Species	Material	GenBankAcc.	Location
Torresitrachia darwini sp. nov.	AM C.463000	GQ443623	NT, ca. 15 km NW of Katherine
Torresitrachia wallacei sp. nov.	AM C.462998	GQ443620	NT, 3.6 km NW of Katherine
Torresitrachia cuttacutta sp. nov.	AM C.462999	GQ443622	NT, 28 km S of Katherine
Torresitrachia alenae sp. nov.	AM C.462997	GQ443621	NT, 10 km NW of Katherine
Torresitrachia weaberana Solem, 1980	AM C.447629	GQ443625	WA, N of Kununurra
	AM C.460986	GQ443624	WA, NE of Kununurra, Weaber Ranges
Torresitrachia cf. *weaberana* Solem, 1980	AM C.462760	GQ443627	NT, Victoria River District
Torresitrachia cf. *bathurstensis* (E.A. Smith, 1984)	WAM S.37009	GQ443626	WA, Kimberley, Augustus Island
Setobaudinia anatispretia Solem, 1985	AM C.437624	GQ443619	NT, SE Timber Creek
Setobaudinia cf. *hirsuta* Solem, 1985	WAM S.36708	GQ443618	WA, Kimberley, South West Osborn Island
Setobaudinia cf. *interrex* Solem, 1985	WAM S.37031	GQ443617	WA, Kimberley, St. Andrews Island
Damochlora spina Solem, 1985	AM C.460993	GQ443616	WA, Mitchell Plateau
Amplirhagada castra Solem, 1981	AM C.460966	GQ443628	WA, Mitchell Plateau
Amplirhagada varia Solem, 1981	AM C.143841	GQ443629	WA, Mitchell Plateau

Köhler used one sample of each species to investigate genetic characters and assess relationships (Table 1). Braby undertook the spatial analysis and prepared the map (Fig. 14). All authors conferred on the conservation aspects, and the resulting text for these aspects was written by Braby and Willan using discipline-specific ecological terminology. Willan assembled the paper. Counts of shell whorls follow the description of Barker (1999).

Radulae and jaws were extracted manually, soaked in 10% potassium hydroxide solution, rinsed in fresh water, and mounted on carbon specimen tabs for scanning electron microscopy. The radular tooth formula shows the numbers of teeth as follows: C (central row of teeth) + number of lateral rows of teeth + number of transitional rows of teeth + number of marginal rows of teeth. Generally, we could observe only subtle differences in tooth and jaw morphology between the species and, given the small number of individuals we examined anatomically, we present our data here but have refrained from evaluating them. This is because the differences seem to be largely individual, while the overall tooth and jaw morphology is highly conservative.

The geographical distribution of land snails and extent of the Tindall Limestone Formation at Katherine was plotted on a spatial map using ArcGIS 9, ArcMap Version 9.2 software. The Geographic Information System (GIS) for geological layers of the Katherine region, supplied by the Northern Territory Geological Survey department, was derived from the Katherine 1:250,000 map sheet KA5309. Locations whose co-ordinates were not recorded at the time of collection, or are dubious, were excluded from both the lists of localities given under each species below and the databases used for generation of the map.

DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. A fragment of the mitochondrial 16S rRNA gene was amplified by PCR using the primers 16Scs1 (Chiba 1999) and 16Sbd1 (Sutcharit *et al.* 2007). Reactions were performed under standard conditions with an annealing step of 90s at 55° C. Sequences were aligned by use of Clustal X vs. 2.0 (Larkin *et al.* 2007) with default settings. The aligned sequence data were trimmed to a total length of 790 bp and comprised 16 sequences, including two *Amplirhagada* sequences that were used as the outgroup to root the tree. To reconstruct the phylogram we selected three additional species of *Torresitrachia*, three species of *Setobaudinia*, one species of *Damochlora* and two species of *Amplirhagada* for inclusion (Table 1). The species of *Setobaudinia* and *Damochlora* were selected because they are camaenids with flat shells reminiscent of those of *Torresitrachia*. A phylogenetic tree was reconstructed by application of the Maximum Likelihood algorithm (ML) using the software Treefinder (Jobb *et al.* 2004) with specifications for a general time reversible model of sequence evolution (GTR+I+Γ) as revealed by the hierachical likelihood test implemented in this analysis software.

Institutional abbreviations. AM – Australian Museum, Sydney; NTM – Museum and Art Gallery Northern Territory (formerly Northern Territory Museum, Darwin); VK – private collection of Vince Kessner, Adelaide River, Northern Territory; WAM – Western Australian Museum, Perth.

SYSTEMATICS

Torresitrachia Iredale, 1939

Torresitrachia Iredale, 1939. Gender feminine. Type species, by original designation, *Helix* (*Trachia*) *endeauvourensis* Brazier, 1872 (= *Torresitrachia torresiana* Hombron and Jacquinot, 1841). Recent, Torres Strait, Queensland, Australia.

Nomenclatural remarks. According to B.J. Smith (1992: 162), the name *Torresitrachia* was first proposed by Iredale (1933), but that introduction constituted only

a nomen nudum. It was validly described later by Iredale (1939) and subsequently revised by Solem (1979), who also described various new species from the Kimberley region of Western Australia and adjoining areas of the Northern Territory. Additional species were later added by Solem (1981) from the northern Kimberley and eastern Arnhem Land, and by Solem (1985) from the northern Kimberley. The type species, *Helix endeauvourensis* from the Endeauvour River, northern Queensland, has been treated as a junior synonym of *Torresitrachia torresiana* (Hombron and Jacquinot, 1841) from Ile Toud, Torres Strait, northern Queensland, by Iredale (1938). Whilst agreeing with Iredale with regard to this synonymy, Solem (1979) acknowledged that the relationships of the various nominal species group taxa described from the Torres Strait islands and subsequently synonymised with *T. torresiana* are in need of further scrutiny.

Diagnosis. Shell medium-sized with sunken to slightly elevated spire; umbilicus moderately open to nearly closed. Apical sculpture varying from rather smooth to pustulose or ridged. Teleoconch sculpture may comprise axial ribs or long spines. Shell surface supports pustulose microsculpture consisting of vertical, angled or spiral ridgelets, umbilical walls usually densely covered by setae. Aperture slightly to strongly deflected from axis of coiling, partly covering the umbilicus, with simple to slightly protruded basal lip and very thin parietal callus.

Penis with epiphallus and epiphallic caecum of variable size; inner wall of epiphallus with structures ranging from longitudinal ridges to complex pilasters; epiphallus separated from penial chamber by circular ridge or change in pilasters; inner wall of penial chamber with dense pustulation proximally and longitudinal pilasters distally. Vas deferens enters epiphallus through complex pilasters or pore. Penial sheath absent. Retractor muscle attached to mid-portion of epiphallus. Vagina and free oviduct of moderate length and width. Spermatheceal head expanded, reaching base of albumen gland. Hermaphroditic duct enters laterally on talon.

Distribution. Species of the genus *Torresitrachia* are found across the north of Australia, from Queensland to Western Australia, and also possibly New Guinea (Solem 1981).

Torresitrachia darwini sp. nov.

Figs 1A, 2–4, 14

Material examined. Holotype – NTM P.43053 (ex AM C.463000), 13.2 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, ca. 15 km NW of Katherine, Katherine Rural College (14°23.683′S, 132°8.683′E), in deep leaf litter and under limestone slabs, intact and well-preserved vine thicket vegetation, large isolated limestone outcrop, coll. V. Kessner and M.F. Braby, 11 December 2008. Paratypes – AM C.463000, 32 specimens (of which 5 are cracked) in alcohol, same data as holotype; NTM P.42906, 12 dried shells, same data as holotype.

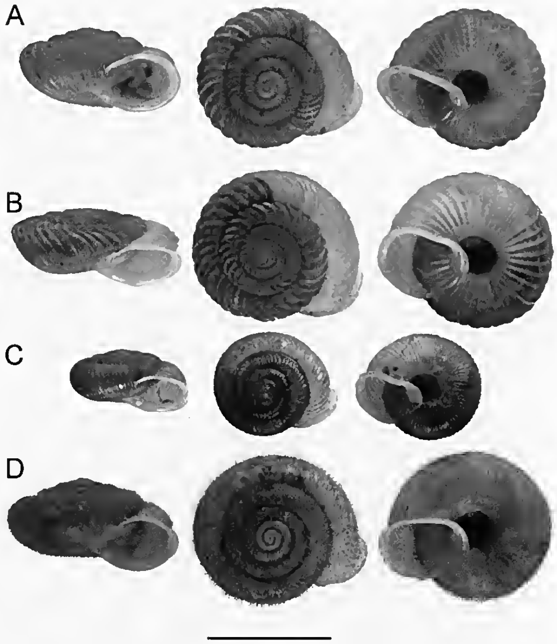

Fig. 1. Shells of holotypes of new *Torresitrachia* species shown in profile (left), dorsally (centre) and ventrally (right): **A**, *T. darwini* sp. nov. NTM P.43053; **B**, *T. wallacei* sp. nov. NTM P.43054; **C**, *T. cuttacutta* sp. nov. NTM P.43055; **D**, *T. alenae* sp. nov. NTM P.43056. Scale = 10 mm.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.42907, 12 dried shells, W Stuart Highway, 13.8 km NW of Katherine, Kintore Caves Reserve (14°24.438, 132°9.2′E), in deep leaf litter, intact and well-preserved vine thicket vegetation, large isolated limestone outcrop, V. Kessner and M.F. Braby, 11 December 2008; NTM P.42908, 8 dried shells, W of Stuart Highway, 3 km SSW of Katherine Rural College (14°23.933′S, 132°8.533′E), on soil surface under limestone rocks, limestone outcrop in open woodland with small patches of shady bushes, coll. V. Kessner, M.F. Braby and R.C. Willan, 25 January 2009; NTM P.42909, 20 dried shells, W of Stuart Highway, 2.6 km SSW of Katherine Rural College (14°23.7′S, 132°8.617′E), crawling on limestone rocks, on a large limestone outcrop with intact and well-developed vine thicket, during rain, at night, coll. V. Kessner and R.C. Willan, 25 January 2009; NTM P.43010, 25 dried shells, W of Stuart Highway, ca. 15 km NW of Katherine (14°23.683′S, 132°8.683′E), on surface of deep leaf litter, in a steep-sided limestone gorge, with intact and well-preserved vine thicket vegetation (tall grasses at mouth of gorge), part of a large isolated limestone outcrop, coll. V. Kessner, M.F. Braby and R.C. Willan, 25 January 2009; VK catalogue no. 12704, 28 dried shells, 3.5 km W of Stuart Highway, 10.2 km NW of Katherine (14°24.75′S, 132°10.333′E), coll. V. Kessner, 1 April 1988; VK catalogue

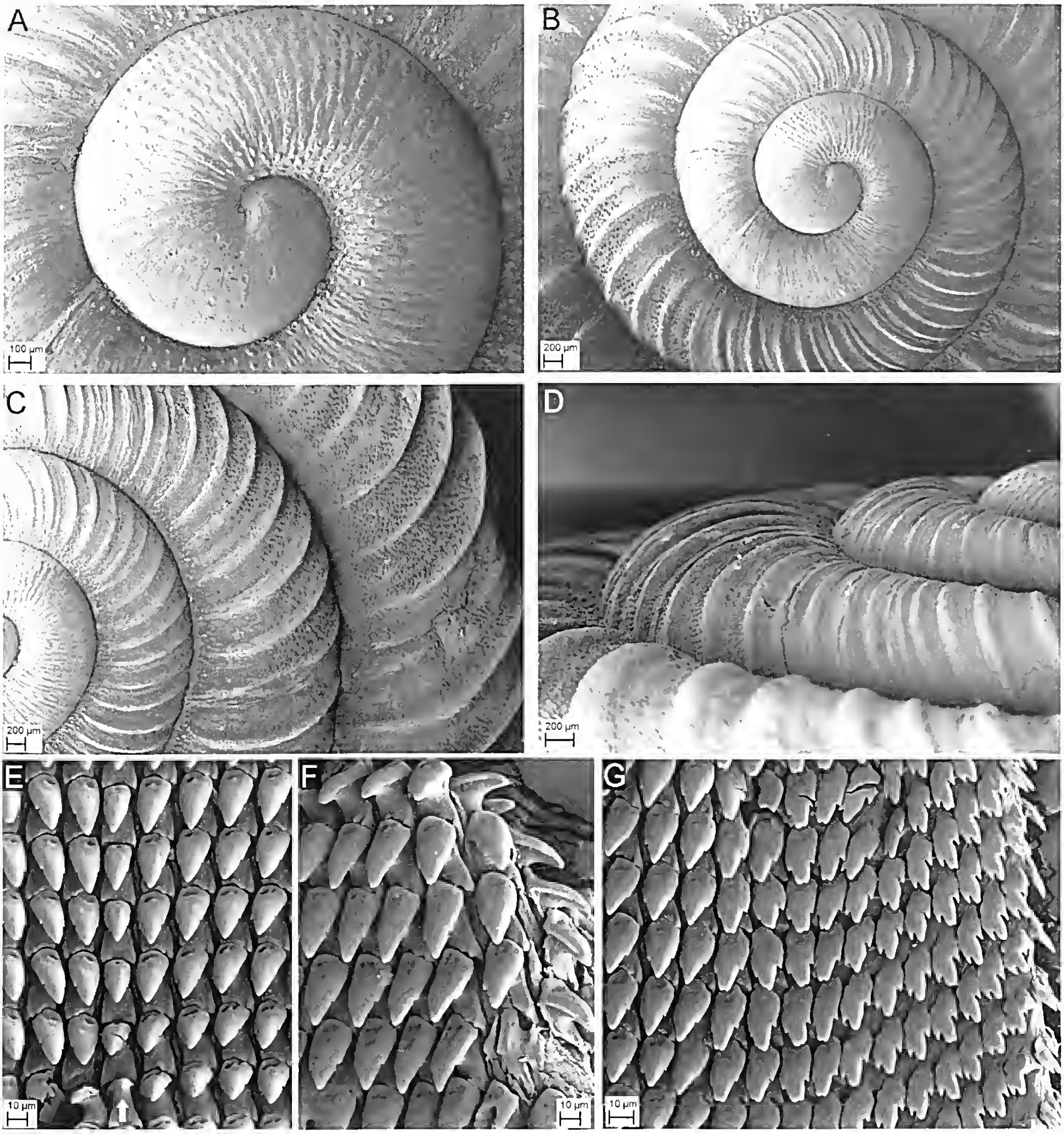

Fig. 2. SEM photographs of shells and radula of *Torresitrachia darwini* sp. nov., paratypes AM C.463000: **A**, Close-up of protoconch (scale 100 µm); **B**, Apical portion of shell with first whorls viewed from above (scale 200 µm); **C**, Sculpture across all whorls of shell viewed from above (scale 200 µm); **D**, Lateral view of shell (scale 200 µm); **E**, Central (white arrow) and inner lateral teeth (scale 10 µm); **F**, Close-up of lateral teeth (scale 10 µm); **G**, Outer lateral and inner marginal teeth (scale 10 µm).

no. 12705, 40 dried shells, W of Stuart Highway, Katherine Rural College, 2.5 km SW of main campus (14°23.5´S, 132°8.5´E), coll. V. Kessner, 1 April 1988; VK catalogue no. 12706, 39 dried shells, W of Stuart Highway, Katherine Rural College, 3.6 km S of main campus (14°24.083´S, 132°8.167´E), coll. V. Kessner, 1 April 1988; VK catalogue no. 29284 NT-126/08, 17 dried shells, same data as holotype; VK catalogue no. 29285 NT-127/08, 17 dried shells, W. of Stuart Highway, 13.8 km NW of Katherine, Kintore Caves Reserve (14°24.438´S, 132°9.2´E), coll. V. Kessner and M.F. Braby, 11 December 2008; VK catalogue no. 29419 NT-005/09, 5 dried shells, W of Stuart Highway, 2.6 km SSW of Katherine Rural College (14°23.7´S, 132°8.617´E), coll. V. Kessner, M.F. Braby and R.C. Willan, 26 January 2009; VK catalogue no. 29420 NT-001/09, 25 dried shells, W of Stuart Highway, 3 km SSW of Katherine Rural College (14°23.933´S, 132°8.533´E), coll. V. Kessner, M.F. Braby and R.C. Willan, 26 January 2009.

Description. Based on 269 specimens.

Shell (Figs 1A, 2A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, with slight angulation at upper whorl, rounded above, rounded to slightly flattened below. Colour uniform, light brownish to horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 2A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch sculpture consisting of pronounced, distinct, regularly spaced axial ribs, curved if viewed from above, elongate and rounded in cross-section; interspaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell though less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Fine granulate periostreal sculpture visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, widely expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 3, 4). Penis coiled, much longer than free anterior part of oviduct; epiphallus moderately long, less than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long, shorter than epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal half of inner penial wall covered with well-developed, large, rhomboid pustules, densely arranged in honey-comb pattern, distal half with 4 to 5, well-developed, longitudinal, smooth pilasters; penial retractor muscle relatively long, still much shorter than penis, innervating more or less at anterior end of epiphallus. Vas deferens rather straight, thin, entering directly into

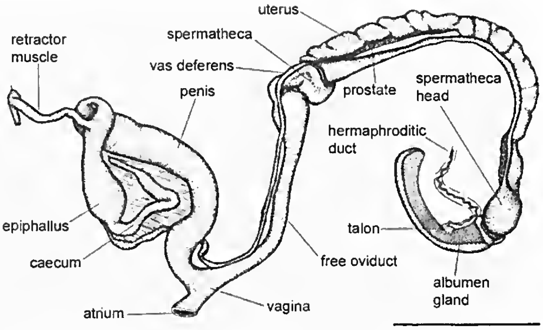

Fig. 3. Genital system of *Torresitrachia darwini* sp. nov. Scale 5 mm.

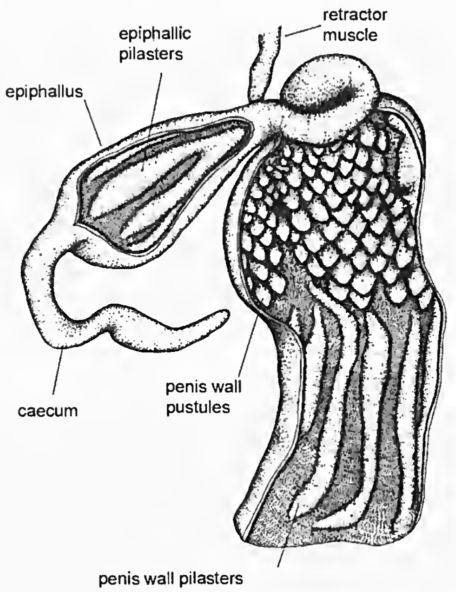

Fig. 4. Detail of penis of *Torresitrachia darwini* sp. nov. Penial wall opened proximally and distally to reveal detail of internal ornamentation. Scale 0.5 mm.

Table 2. Comparative shell measurements for the four species of *Torresitrachia*. Data given as range (mean ± standard deviation) in mm. n = number of specimens measured; **H** = shell height; **D** = maximum diameter of body whorl; **LW** = height of body whorl; **U** = maximum width of umbilicus; **W** = total number of whorls (teleoconch plus protoconch); **H/D** = ratio between height and maximum diameter of shell.

Species	n	H	D	LW	U	W	H/D
T. darwini sp. nov.	9	6.0 – 7.6 (6.9 ± 0.5)	11.8 – 13.5 (12.8 ± 0.6)	5.0 – 6.3 (5.9 ± 0.4)	2.5 – 3.5 (3.1 ± 0.3)	4.5 – 5.0 (4.6 ± 0.2)	0.50 – 0.60 (0.54 ± 0.03)
	Holotype (NTM P.43053)	7.1	13.2	6.3	3.0	4.5	0.54
T. wallacei sp. nov	14	6.4 – 7.3 (6.9 ± 0.3)	12.0 – 13.5 (12.9 ± 0.4)	5.6 – 6.2 (5.9 ± 0.2)	2.5 – 3.2 (3.0 ± 0.2)	4.5 – 4.9 (4.7 ± 0.1)	0.51 – 0.58 (0.53 ± 0.02)
	Holotype (NTM P.43054)	7.0	13.0	6.0	3.0	4.7	0.54
T. cuttacutta sp. nov.	7	4.3 – 5.3 (5.0 ± 0.3)	9.3 – 10.9 (10.0 ± 0.5)	4.1 – 4.6 (4.4 ± 0.2)	2.0 – 2.7 (2.4 ± 0.2)	3.0 – 3.6 (3.4 ± 0.2)	0.46 – 0.53 (0.50 ± 0.03)
	Holotype (NTM P.43055)	5.0	10.1	4.5	2.5	3.5	0.50
T. alenae sp. nov.	9	5.9 – 7.5 (6.6 ± 0.5)	12.5 – 14.0 (13.2 ± 0.5)	5.3 – 6.3 (5.8 ± 0.3)	2.5 – 3.5 (3.0 ± 0.3)	4.5 – 5.1 (4.7 ± 0.2)	0.46 – 0.54 (0.50 ± 0.03)
	Holotype (NTM P.43056)	7.5	14.0	6.3	2.9	4.9	0.54

epiphallus through pore. Vagina tubular, posteriorly inflated, rather long, interior with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct differentiated, duct moderately wide, inner wall with longitudinal pilasters, head narrowly elongated with markedly inflated tip, wall thin, inside densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus much longer than anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Figs 2E–G). Ribbon rectangularly elongate, on average 2.0 ± 0.0 mm long, with an average 72 ± 5 rows of teeth, 36.1 ± 2.6 rows/mm (n = 2). Tooth formula C + 9 –12 + 3–4 + 12–14. Central teeth with sharply pointed, elongate, triangular mesocones, of about as same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of 2.6 km^2. One population occurs within the Kintore Caves Nature Reserve.

Comparative remarks. Among all the species described herein, *Torresitrachia darwini* sp. nov. has by far the shortest radula with the fewest number of rows. It is most similar to *T. wallacei* sp. nov. overall. Compared with this species however, the shell is larger (Table 2) and proportionately higher (larger H/D ratio, see Table 2), the angle between the axis of coiling and the aperture is considerably smaller and the last whorl is not as angulate. Compared with *T. alenae* sp. nov., this species differs most conspicuously in shell sculpture (i.e., in possessing ribs rather than hairs). Shells of *T. cuttacutta* sp. nov. exhibit much denser and finer ribbing, the inner penial wall has finer, less regularly and densely arranged pustules, and the spermatheeal head is not inflated.

Etymology. We name this species in honour of Charles Robert Darwin (1809–1882) on the 150th anniversary of publication of his seminal work *On the origin of species by means of natural selection*...(Darwin 1859). Darwin's interests lay in the biogeography and dispersal of freshwater and terrestrial molluscs and he undertook experiments with land snails to elucidate the mechanisms that may have brought them to oceanic islands (Örstan and Dillon 2009).

Torresitrachia wallacei sp. nov.

Figs 1B, 5–7, 14

Material examined. Holotype – NTM P.43054 (ex AM C.462998), 13.0 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, 3.6 km NW of Katherine (14°26.64′S, 132°14.28′E), under limestone slabs, open low limestone outcrops and sinkholes with scattered Rock Fig trees (*Ficus platypoda*) and by tall annual speargrass (*Sorghum macrospermum*), coll. V. Kessner, 25 January 2009. Paratypes – AM C.462998, 3 specimens in alcohol (of which 2 are cracked), same data as holotype; NTM P.42964, 8 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.7846, 6 dried shells, Kintore Reserve, N part of Kintore Caves system, in sediments, limestone cave outwash, coll. P. Bannink, 30 May 1993; NTM P.26178, 1 dried shell 12 km NE of Katherine, sorted from leaf debris, in mouth of a cave, coll. P. Bannink, 5 May 1994; NTM P.37748, 1 dried shell, Kintore Reserve, N part of Katherine Caves system, in leaf litter, at entrance to a cave, coll. P. Bannink, 4 September 1993; NTM P.37774, 3 dried shells, 10 km N of Katherine, N part of Katherine Caves system, in flood debris, on floor of a cave, coll. P. Bannink, 5 May 1994; NTM P.37778, 3 dried shells, 10 km N of Katherine, N part of Katherine Caves system, in flood debris, on floor of a cave, coll. P. Bannink, 21 May 1994; NTM P.42903, 8 dried shells, W of Stuart Highway, 3.7 km NW of Katherine (14°26.8′S, 132°14.28′E), under limestone slabs, low limestone outcrops and sinkholes with scattered Rock Fig trees (*Ficus platypoda*), coll. V. Kessner and M.F. Braby, 11 December 2008; NTM P.43070, 18 dried shells, limestone outcrop between Florina Road and Tokmakoff Road (14°28.433′S, 132°13.85′E) 'free sealer' under limestone rocks, in a low open limestone outcrop, coll. V. Kessner, 4 August 1986; VK catalogue no. 555, 12 dried shells, 1 km W of Stuart Highway, 3 km NW of Katherine (14°26.867′S, 132°14.05′E), coll. V. Kessner, 15 February 1980; VK catalogue no. 577, 4 dried shells, E of Stuart Highway, 4 km NW of Katherine (14°26.433′S, 132°14.267′E), coll. V. Kessner, 3 March 1979; VK catalogue no. 589, 7 dried shells, 0.5 km W of Stuart Highway, 3 km NW of Katherine (14°26.783′S, 132°14.767′E), coll. V. Kessner, 3 March 1979; VK catalogue no. 9417, 1 dried shell, E of Stuart Highway, 3 km NW of Katherine (14°26.533′S, 132°14.283′E), coll. V. Kessner, 4 August 1986; VK catalogue no. 9352 NM-010, 64 dried shells, limestone hillock near Springvale Homestead (14°29.963′S, 132°13.667′E), coll. V. Kessner, 20 May 1986; VK catalogue no. 9493, 27 dried shells, E of Stuart Highway, 3 km NW of Katherine (14°26.533′S, 132°14.283′E), coll. V. Kessner, 4 August 1986; VK catalogue no. 9494, 19 dried shells, limestone outcrop between Florina Road and Tokmakoff Road (14°28.433′S, 132°13.85′E) 'free sealer' under limestone rocks, in a low open limestone outcrop, coll. V. Kessner, 4 August 1986; VK catalogue no. 27325 NT-07/05, 9 dried shells, E of Stuart Highway, 3.3 km NW of Katherine (14°26.443′S, 132°14.133′E), coll. V. Kessner, 4 June 2005; VK catalogue no. 29286 NT-002/09, 7 dried shells, same data as holotype; VK catalogue no. 29293 NT-125/08, 4 dried shells, W of Stuart Highway, 3.6 km NW of

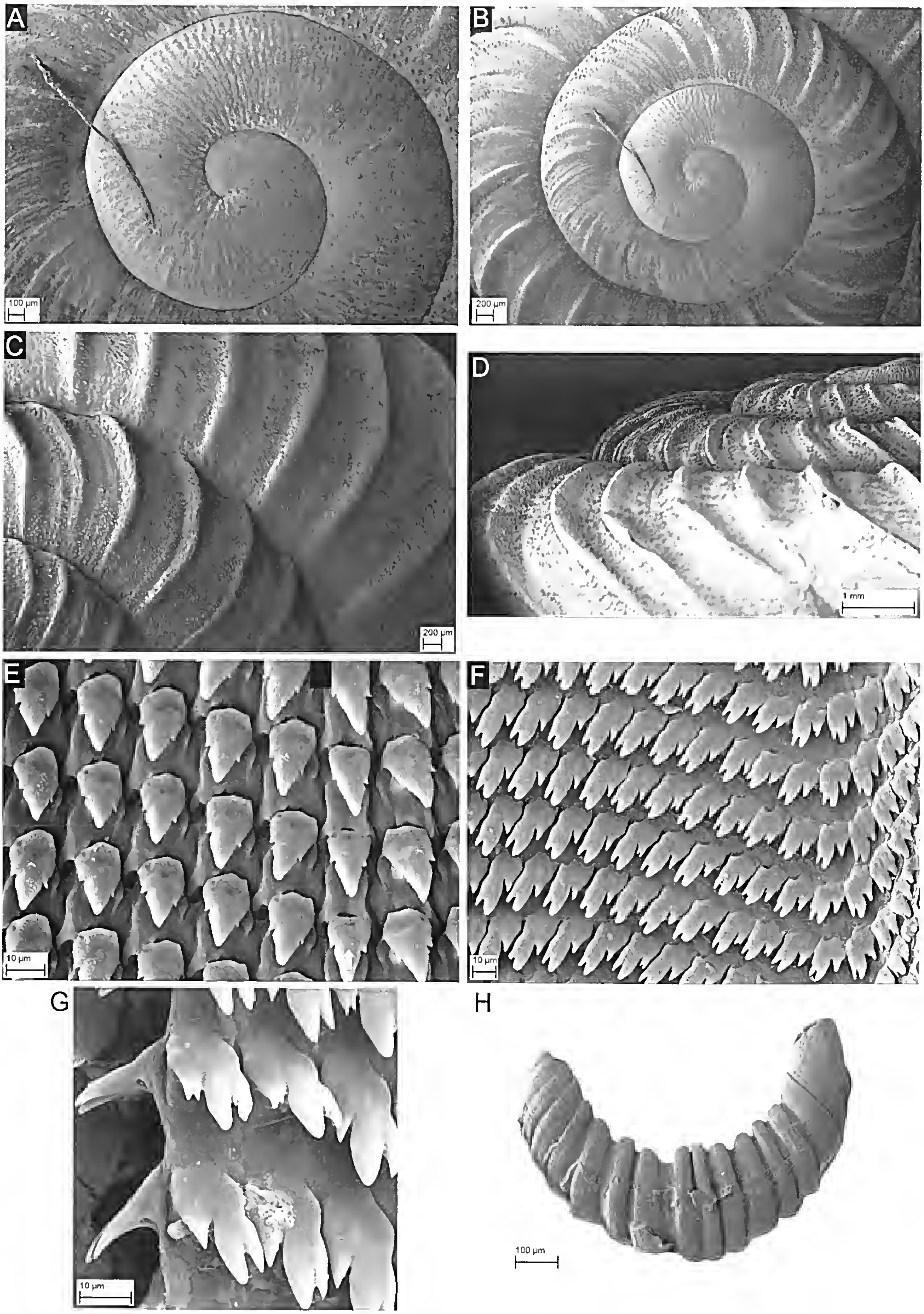

Figure 5. SEM photographs of shells, radula and jaws of *Torresitrachia wallacei* sp. nov., paratypes AM C.462998: **A,** Close-up of protoconch (scale 100 µm); **B,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **C,** Sculpture on second to fourth whorls viewed from above (scale 200 µm); **D,** Lateral view of shell (scale 1 mm); **E,** Close-up of central (white arrow) and inner lateral teeth (scale 10 µm); **F,** Inner and middle marginal teeth (scale 10 µm); **G,** Close-up of middle marginal teeth (scale 10 µm); **H,** Jaw (scale 100 µm).

Katherine (14°26.8´S, 132°14.283´E), coll. V. Kessner and M.F. Braby, 11 December 2008.

Description. Based on 174 specimens.

Shell (Figs 1B, 5A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, rounded to slightly angulate at upper whorl. Colour uniform, light brownish horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 5A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch sculpture consisting of strong, distinct, regularly spaced axial ribs, curved at shell angulation if viewed from above, elongately rounded in cross-section; interspaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell, less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Shell sparsely covered with fine granulate periostracal sculpture, visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 6, 7). Penis coiled, longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long – about as long as epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal third of inner penial wall covered with well-developed, rather large, rhomboid pustules, arranged in honey-comb pattern, distal two-thirds with 4 to 5, longitudinal, smooth pilasters; penial retractor muscle very short, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, moderate in length, with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct slightly differentiated, duct wide, inner wall with longitudinal pilasters, head narrowly elongate, tip slightly inflated with tubular to pyriform tip, wall thin, interior densely ciliated. Free oviduct rather short, coiled underneath entrance to uterus. Uterus of about same length as anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

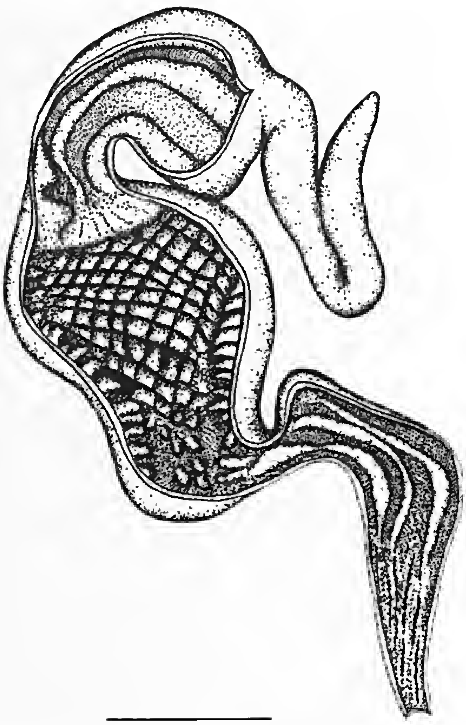

Fig. 7. Detail of penis of *Torresitrachia wallacei* sp. nov. Penial wall opened along its length to reveal detail of internal ornamentation. Scale 1 mm. See Fig. 4 for labelling of structures.

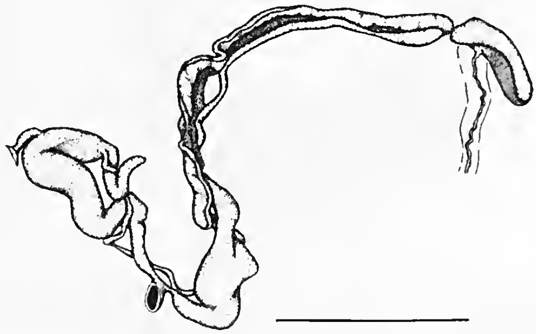

Fig. 6. Genital system of *Torresitrachia wallacei* sp. nov. Scale 5 mm. See Fig. 3 for labelling of organs.

Radula (Figs 5E–G). Ribbon rectangularly elongate, on average 3.0 ± 0.5 mm long, with an average 126 ± 18 rows of teeth, 42.8 ± 0.9 rows/mm (n = 2). Tooth formula C + 10–12 + 3–4 + 10–12. Central teeth with sharply pointed, elongate, triangular mesocones, of about as same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones, split into 2 denticles.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of 4.9 km^2. No population occurs within any reserve.

Comparative remarks. The most distinctive feature of *Torresitrachia wallacei* is its depressed spire so that the upper surface of the shell is almost flat. Comparisons with the other species, particularly with *T. darwini* its closest relative, are given elsewhere in this paper.

Etymology. We name this species in honour of Alfred Russel Wallace (1823–1913) for independently proposing a theory of natural selection (Wallace 1870).

Torresitrachia cuttacutta sp. nov.

Figs 1C, 8–10, 14

Material examined. HOLOTYPE – NTM P.43055 (ex AM C.46299), 10.1 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, W of Stuart Highway, 28 km S of Katherine (14°32.167′S, 132°25.467′E), under limestone rocks, in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 26 January 2009. PARATYPES – AM C.462999, 5 specimens in alcohol (of which 3 are cracked), same data as holotype; NTM P.42905, 20 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, S of Katherine). NTM P.37773, 9 dried shells, NTM P.37831, Cutta Cutta Caves (14°32.7′S, 132°25.8′E), in flood debris, on floor of a cave, coll. P. Bannink, 1 April 1994; NTM P.37836, 1 dried shell, Cutta Cutta Caves, Cutta Cutta Cave, in bark, 350 metres inside a cave, coll. A. Clarke, 1 April 1996; NTM P.37836, 1 dried shell, Cutta Cutta Caves, Water Resources Cave (14°32.7′S, 132°22′E), in deposits on floor of a cave, coll. A. Clarke, 2 April 1996; NTM P.9385, 7 dried shells, Cutta Cutta Caves, Tindal Cave (14°31′S, 132°25.8′E), in leaf litter, under a log, inside a cave, coll. S. Bone, 16 January 1997; VK catalogue no. 2168, 58 dried shells, W of Stuart Highway, 19 km S of Katherine (14°31.8′S, 132°25.617′E), coll. V. Kessner, 6 January 1979; VK catalogue no. 8222, 3 dried shells, Cutta Cutta Caves, 16 Miles Caves (14°34.7′S, 132°28.15′E), coll. V. Kessner, 19 June 1978; VK catalogue no. 9499, 30 dried shells, 19.3 km S of Katherine, W of Stuart Highway (14°32.233′S, 132°25.00′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9710, 90 dried shells, 19.3 km S of Katherine, W of Stuart Highway (14°32.233′S, 132°25.00′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9456 NW-002, 37 dried shells, 19.4 km S of Katherine W of Stuart Highway (14°31.417′S, 132°25.5′E), coll. V. Kessner, 2 August 1986; VK catalogue no. 9454 NW-009, 29 dried shells, 3 km W of Stuart Highway, Cutta Cutta Caves, Guy's Cave (14°34.983′S, 132°27.383′E), coll. V. Kessner, 19 May 1986; VK catalogue no. 12709, 4 dried shells, 24 km S of Katherine, 1.5 km W of Stuart Highway (14°33.617′S, 132°26.95′E), coll. V. Kessner, 1 April 1988; VK catalogue no. 3483, 11 dried shells, Tindal, Maud Creek Road, E of Katherine, N of Stuart Highway (14°28.7′S, 132°24.333′E), coll. P.A. Barden, 11 May 2007; VK catalogue no. 29288, 19 dried shells, same data as holotype.

Description. Based on 287 specimens.

Shell (Figs 1C, 8A–E). Relatively small (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl narrow to moderate, rounded with slight angulation at upper whorl. Colour uniform, light yellowish-brownish to horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 8A) rather smooth, sparsely covered with smooth, flattened pustules. Teleoconch sculpture consisting of narrow, distinct, regularly spaced axial ribs, slightly curved if viewed from above, squarish to rounded in cross-section; spaces between axial ribs wider than thickness of ribs; ribs almost evenly distributed across shell, less pronounced on first whorl, rib height reduced towards suture, ribs absent from umbilical sector. Shell very sparsely covered with fine granulate periostracal sculpture, visible only under high magnification; hairs and/or filaments absent. Aperture wide; outer lip rounded to slightly excavated, sharp, widely expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 9, 10). Penis coiled, not much longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, long, shorter than epiphallus, with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal third to half of inner penial wall covered with well-developed, rather small, rounded pustules, sparsely and irregularly arranged, distal two thirds to half with 4, rather thin, longitudinal, smooth pilasters; penial retractor muscle stubby, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, moderate in length, interior with longitudinal pilasters. Spermatheca long, reaching base of albumen gland; head and duct differentiated, duct moderately wide, inner wall with longitudinal pilasters, head narrowly elongated with uninflated tip, wall thin, inside densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus about as long as anterior part of oviduct. Albumen gland much shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Figs 8F–H). Ribbon rectangularly elongate, on average 2.3 mm long, with an average 101 rows of teeth, 44.7 rows/mm (n = 1). Tooth formula C + 9 –12 + 3–4 + 12–14. Central teeth with sharply pointed, elongate, triangular mesocones, of about same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones.

Distribution. Endemic to the Tindall Limestone Formation (Fig. 14); occurring south of the Katherine River.

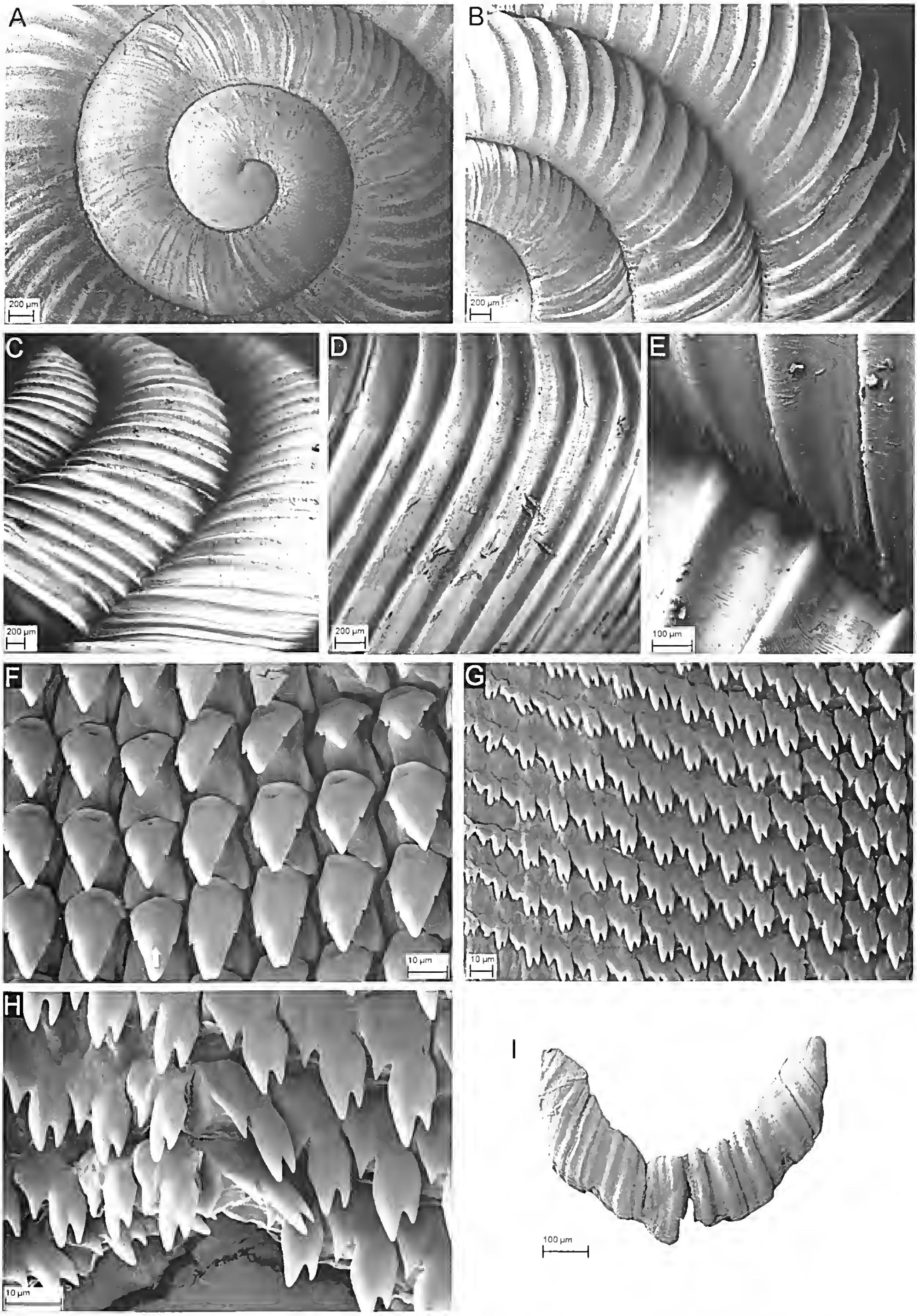

Figure 8. SEM photographs of shells, radula and jaws of *Torresitrachia cuttacutta* sp. nov., paratypes AM C.462999: **A**, Apical portion of shell with first whorls viewed from above (scale 200 µm); **B**, Surface across all whorls of shell as viewed from above (scale 200 µm); **C**, Surface of third to fifth whorls viewed obliquely from above (scale 100 µm); **D**, Close-up of sculpture on body whorl (scale 200 µm); **E**, Details of sculpture at suture between body and penultimate whorl; **F**, Close-up of central (white arrow) and inner lateral teeth (scale 10 µm); **G**, inner and middle marginal teeth (scale 10 µm); **H**, Close-up of middle marginal teeth (scale 10 µm); **I**, Jaw (scale 100 µm).

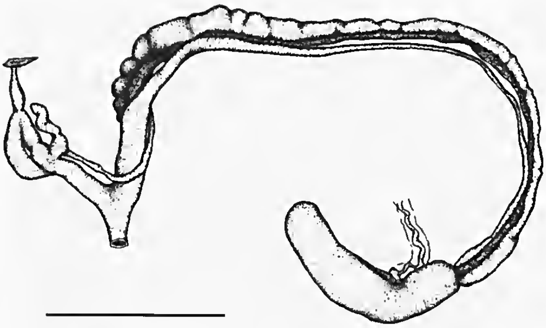

Fig. 9. Genital system of *Torresitrachia cuttacutta* sp. nov. Scale 2.5 mm. See Fig. 3 for labelling of organs.

Present collections indicate an extent of occurrence of 20.4 km^2. One population occurs within the Cutta Cutta Caves Nature Reserve.

Comparative remarks. *Torresitrachia cuttacutta* sp. nov. is distinguished by its relatively small shell size (smaller when adult than any of the other three species). Compared to the three other species described herein it has finer axial ribs that are not as strongly elevated and are arranged more densely, the body whorl lacks angulation, and the lower part of body whorl is not as flattened. Furthermore, the pustulation of the inner penial wall is less developed, the pustules are not as densely packed, they are smaller and arranged randomly rather than in a honey-comb pattern, the penial pilasters are much smaller and thinner, and the uterus is much longer. The radular ribbon tends to be slightly shorter than in *T. wallacei* sp. nov. and it has fewer rows of teeth. Compared with *T. alenae* sp. nov., it differs most conspicuously in its shell sculpture (i.e., it possesses axial ribs instead of hairs).

Etymology. We name this species after its type locality, Cutta Cutta. It is intended as a noun in apposition.

Torresitrachia alenae sp. nov.

Figs. 1D, 11–13, 14

Material examined. Holotype – NTM P.43056 (ex AM C.462997), 14.0 mm diameter (other measurements given in Table 2), Australia, Northern Territory, Katherine District, E of Stuart Highway, 10 km NW of Katherine (14°24.367′S, 132°11.783′E), aestivating in leaf litter, under limestone rocks, in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 26 January 2009. Paratypes – AM C.462997, 21 specimens in alcohol (of which 5 are cracked), same data as holotype; NTM P.42904, 15 dried shells, same data as holotype.

Additional (non-type) material (all Northern Territory, Katherine District, N of Katherine). NTM P.37736, 2 dried shells, 7 km N of Katherine, northern part of Katherine Caves system, in fig tree leaf litter on floor of a cave shaft, coll. P. Bannink, 7 May 1994; NTM P.37740, 1 dried shell, 7 km N of Katherine, northern part of Katherine Caves system, in leaf litter, cave flood debris, coll. P. Bannink, 7 May 1994; VK catalogue no. 29287, 24 dried shells, same data as holotype; VK catalogue no. 548, 26 dried shells, E of Stuart Highway, 10 km NW of Katherine (14°24.75′S, 132°12.5′E), in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 28 February 1979; VK catalogue no. 8602, 10 dried shells, E of Stuart Highway, 11 km NW of Katherine (14°24.167′S, 132°11.3′E), in small patches of vine thicket on limestone outcrops, in open woodland, coll. V. Kessner, 20 March 1986.

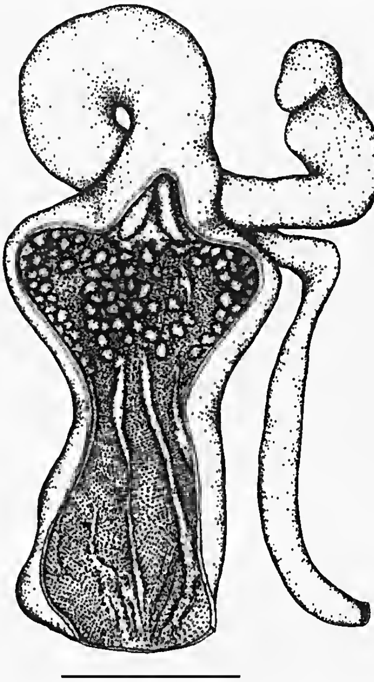

Fig. 10. Detail of penis of *Torresitrachia cuttacutta* sp. nov. Penial wall opened distally to reveal detail of internal ornamentation. Scale 0.5 mm. See Fig. 4 for labelling of structures.

Description. Based on 97 specimens.

Shell (Figs 1D, 11A–D). Medium sized (Table 2), almost flat with low spire, thin, transparent. Diameter of last whorl moderate, angulate at upper whorl, rather flattened above and rounded below angulation. Colour uniform, light brownish horn; inner lip whitish. Umbilicus open, moderately wide (interior whorls visible), only slightly covered by outer lip. Protoconch (Fig. 11A) covered with dense, smooth, flattened pustules arranged in axial rows. Teleoconch smooth except for faint axial growth lines; shell covered by hairs – density of hairs greatest on body whorl, quickly decreasing on penultimate whorl, and very sparse or absent on first whorl; hairs regularly distributed across whorl diameter, decreasing underneath suture, not present on umbilical sector of whorls where they are replaced by setae; no periostracal nodules on shell surface. Aperture wide; outer lip rounded

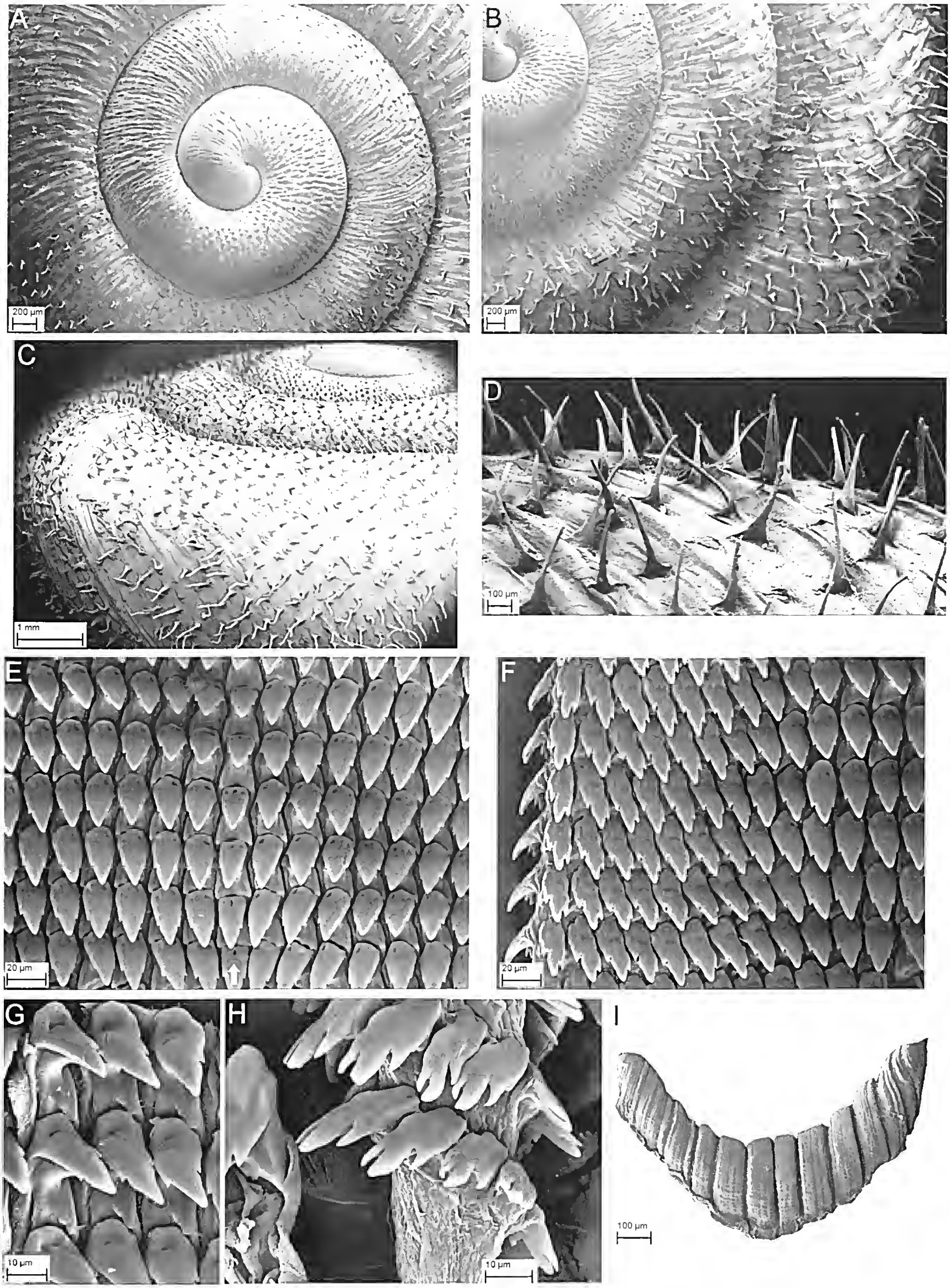

Fig. 11. SEM photographs of shells, radula and jaws of *Torresitrachia alenae* sp. nov., paratypes AM C.462997: **A,** Apical portion of shell with first whorls viewed from above (scale 200 µm); **B,** Surface across all whorls of shell as viewed from above (scale 200 µm); **C,** Lateral view of body whorl (scale 1 mm); **D,** Close-up of hairs on body whorl (scale 100 µm); **E,** Central (white arrow) and lateral teeth (scale 10 µm); **F,** Outer lateral and inner marginal teeth (scale 20 µm); **G,** Close-up of inner lateral teeth (scale 10 µm); **H,** Close-up of middle marginal teeth (scale 10 µm); **I,** Jaw (scale 100 µm).

to slightly excavated, sharp, expanded, not or only slightly reflected, basal node of lip very weakly developed, parietal wall of inner lip inconspicuous.

Pallial cavity. Deep, comprising last whorl. Mantle pigmentation spotted to mottled, black. Kidney comprising half of mantle cavity.

Genitalia (Figs 12, 13). Penis coiled, much longer than free anterior part of oviduct; epiphallus moderately long, half or more than half of entire penial length, inner wall with 4 longitudinal pilasters, pustules absent; epiphallic caecum curved, very long, longer than epiphallus, inner wall with longitudinal pilasters; epiphallus separated from penial chamber by crescent-shaped thickening and change in pilasters; proximal three-quarters of inner penis wall covered with well-developed, rhomboid pustules, arranged in honey-comb pattern, distal part with 4 longitudinal, smooth pilasters; penial retractor muscle very short, innervating at mid-portion of epiphallus. Vas deferens rather straight, thin, entering directly into epiphallus through pore. Vagina tubular, posteriorly inflated, short, interior with broad longitudinal pilasters with transverse corrugations. Spermatheca long, reaching base of albumen gland; head and duct slightly differentiated, duct wide, inner wall with longitudinal, corrugated pilasters, head narrowly elongated, with inflated, club-like tip, wall thin, interior densely ciliated. Free oviduct very short, coiled underneath entrance to uterus. Uterus of about same length as anterior part of oviduct or slightly longer. Albumen gland shorter than uterus. Talon embedded into anterior half of albumen gland, receiving hermaphroditic duct laterally.

Radula (Fig. 8E–H). Ribbon rectangularly elongate, on average 2.7 ± 0.3 mm long, with an average 106 ± 10 rows of teeth, 39.1 ± 0.2 rows/mm (n = 2). Tooth formula C + 14 + 1–2 + 12. Central teeth with sharply pointed, elongate, triangular mesocones, of about same length as base of tooth; central ectocones tiny, pointed. Lateral mesocones of about same size and shape as central mesoncones; ectocones pointed, tiny; endocones slightly smaller than extocones. Marginal teeth with elongate mesocones; endocones smaller and narrower than mesocones; ectocones shorter than endocones, split into 2 denticles.

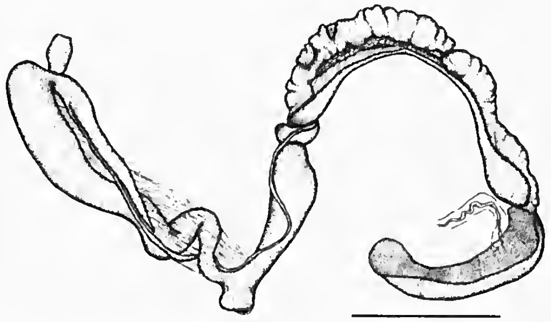

Fig. 12. Genital system of *Torresitrachia alenae* sp. nov. Scale 5 mm. See Fig. 3 for labelling of organs.

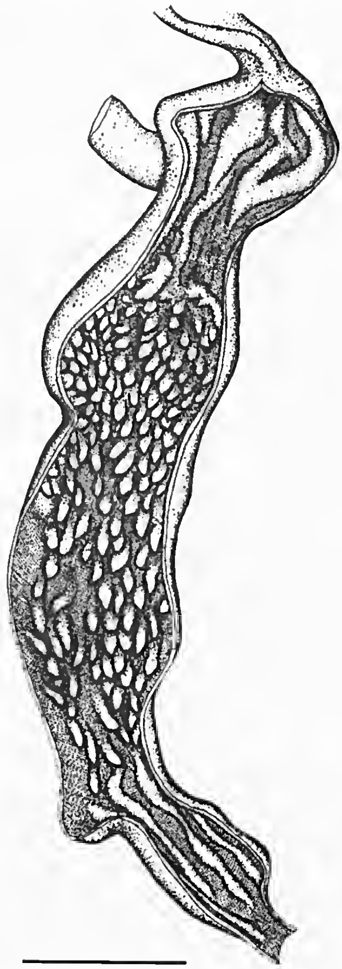

Fig. 13. Detail of penis of *Torresitrachia alenae* sp. nov. Penial wall opened along its length to reveal detail of internal ornamentation. Scale 1.5 mm. See Fig. 4 for labelling of structures.

Distribution. Endemic to the Tindall Limestone formation (Fig. 14); occurring north of the Katherine River. Present collections indicate an extent of occurrence of only less than 1.0 km^2. No population occurs within any reserve.

Comparative remarks. *Torresitrachia alenae* is the only one of the four species described herein to lack axial sculpture and to have periostracal hairs on the shell surface. The pustulation on the inner penial wall is much longer than in any of the other species. The radular ribbon tends to be slightly shorter than in *T. wallacei* sp. nov., with fewer rows of teeth, and with slightly fewer rows of teeth per mm.

Etymology. We name this species in honour of Alena Kessner, wife of Vince Kessner, in recognition of her support through many years of Vince's molluscan obsession, both in the field and at home.

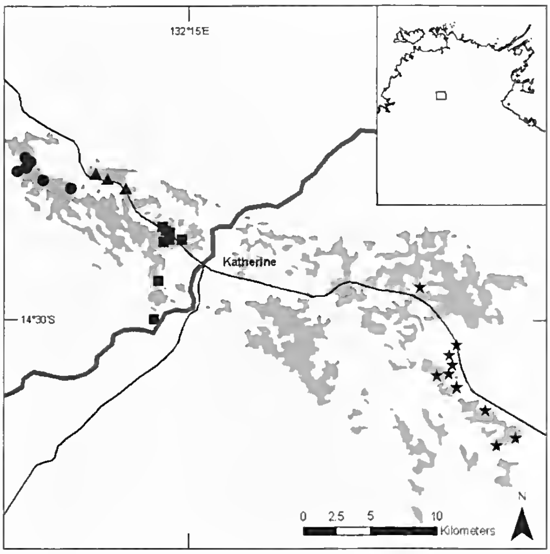

Fig. 14. Distribution map of *Torresitrachia* species: ● = *T. darwini* sp. nov.; ■ = *T. wallacei* sp. nov.; ★ = *T. cuttacutta* sp. nov.; ▲ = *T. alenae* sp. nov. Limestone outcrops are represented by shaded areas. The thick line represents the Katherine River and the thin lines represent major highways.

DISCUSSION

Three of the new species – *Torresitrachia darwini*, *T. wallacei* and *T. cuttacutta* – are morphologically (i.e., conchologically and anatomically) very close to each other. There are subtle and consistent differences between them, but as their populations are allopatric these differences could be due to intraspecific variation. However, their status as separate species is strongly supported by the degrees of genetic differentiation, with genetic distances between them ranging well above 10% (Fig. 15, Table 3). This is more than one would expect within the limits of a single species and together with the consistent differences in morphology, we can assume that there are probably four distinct species. *Torresitrachia darwini* and *T. wallacei* appear to be sister species, and *T. cuttacutta* is relatively close to them. Only *T. alenae* is clearly different by having hairs instead of axial ribs, and is only distantly related genetically.

The four species of *Torresitrachia* described here are united both geographically in their occurrence in the Katherine District and also ecologically in being apparently the only species of the genus obligately associated with limestone (calcium carbonate). According to our field observations, all are 'free sealers' in that they survive the long dry season in the litter or soil and seal the aperture with a calcified mucous covering (an epiphragm) that is porous yet offers protection from desiccation (Stanisic 2008).

Limestone outcrops in the 'wet-dry' tropics can be viewed as important refugia for the survival of land snails and the snails themselves are surrogates for measuring biodiversity conservation in the ecological communities in their specialised habitats (Stanisic 1999; Stanisic and Ponder 2004; Cameron *et al.* 2005; Slatyer *et al.* 2007). These limestone outcrops occur mainly in the drier inland areas of the monsoonal topics of northern Australia and their occurrence is sporadic. The outcrops frequently support pockets of dry rainforest (deciduous monsoon vine thickets) amidst a 'sea' of savannah woodland. Presumably the snails' dependence on limestone is related to the fact that calcium, which is readily available in these habitats, is required for shell growth and reproduction (Graveland *et al.* 1994). Thus these limestones afford the snails protection during the dry season when they are aestivating and an abundant source of calcium during the wet season when they are feeding and breeding.

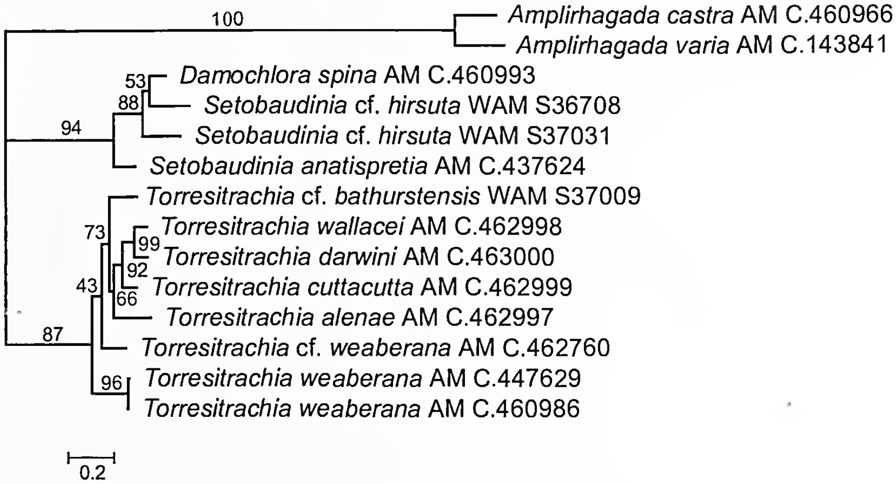

Fig. 15. Maximum Likelihood tree based on analysis of a partial fragment of the mitochondrial 16S rRNA gene (length of unaligned sequences approx. 750 bp) for a general time-reversible model of sequence evolution with gamma-distributed rate heterogeneity (GTR+I+Γ). Numbers on branches indicate nodal support by expected likelihood weights to all rearrangements of tree topology (WLW-LR; Strimmer and Rambaut 2002).

Table 3. Pair-wise genetic distances between the four *Torresitrachia* species. Corrected distances vary from 9.6% to 22.0%. Figure in upper rows = uncorrected p-distances; figure in lower row = corrected Tamura-Nei distances (Tamura and Nei 1993).

	T. alenae sp. nov.	*T. cuttacutta* sp. nov.	*T. darwini* sp. nov.
T. wallacei sp. nov.	0.165 0.220	0.101 0.121	0.082 0.096
T. alenae sp. nov.		0.149 0.194	0.158 0.207
T. cuttacutta sp. nov.			0.115 0.140

When the woodland surrounding these limestone outcrops is intact, densities of these land snails can be high (in the order of dozens per square metre), as at the type locality of *Torresitrachia darwini*. However, increased fire frequency, replacement of the existing forest by (native and introduced) annual grasses, reduction/elimination of the canopy, and high stocking rates of cattle during the wet season can reduce densities of these land snails dramatically (Woinarski *et al.* 2007) as at the type locality of *T. wallacei*. Fortunately there is no quarrying of the limestone for cement production as happens in other parts of Australia (e.g., Stanisic and Ponder 2004), South-East Asia (Clements *et al.* 2006) and many other parts of the world.

Fires pose the greatest threat to land snails (Stanisic and Ponder 2004), both generally and at the locations where these new taxa are found (Braby *et al.* In prep.). Fires affect snails directly by incineration and by dehydration, and indirectly through the destruction of their microhabitat (reduction of litter on the forest floor and soil moisture) (Stanisic and Ponder 2004; Stanisic 2008: 10). Fires now occur more frequently (probably annually close to the city of Katherine and near the Katherine River) than they did in the past. The grasses whose growth is promoted by fires increase the fuel load, which increases fire severity (frequency and/or intensity) and this leads to increased disturbance and decreased tree cover, which then facilitates further growth of grass. This cycle is known as the 'grass/fire cycle' (D'Antonio and Vitousek 1992). It may take many years for a fire-ravaged habitat to recover. Since the *Torresitrachia* snails in their limestone refugia are sensitive to desiccation, have poor tolerance to high temperatures and have no capacity to escape the fires (especially during the dry season when they are aestivating) (pers. obs.) they are going to be severely impacted by the 'grass/fire cycle' combined with habitat loss. Unless there is improved land management on the limestone outcrops in the Katherine district through fire suppression and control of grasses, some of the most localised of these limestone obligate *Torresitrachia* species, such as *T. wallacei* and *T. alenae*, may become extinct very soon (Braby *et al.* In prep.). They are certainly already seriously threatened.

Besides the snails of the genus *Torresitrachia* described herein, the miniscule pupillid snail *Gyliotrachela australis* (Odhner, 1917) is another limestone obligate restricted to the Katherine and Victoria River Districts. Other camaenids belonging to the genera *Xanthomelon* and *Setobaudinia* are endemic to the Katherine District, but are not restricted to limestones. They are not described yet, but are also already threatened by the same processes affecting the *Torresitrachia* species.

ACKNOWLEDGEMENTS

Peter Bannink, an ardent, Darwin-based speleologist, made collections of invertebrates from the caves he and his companions (Arthur Clarke and Sharon Bone) were exploring in the Katherine District in the 1990s and kindly donated them to the NTM. Peter's collections contain numerous land snails, including several species of *Torresitrachia*. The limestone outcrops where these new *Torresitrachia* snails occur contain fossil land snails and we are very grateful to Dirk Megirian for collecting some modern snails for the NTM mollusc collection during his palaeontological studies, including *T. wallacei*. We thank Brian Heim, Manager of Charles Darwin University's Katherine Campus, on which grounds the Katherine Rural College is located, for access to the limestone outcrops on that site. Philip Short of the Darwin Herbarium kindly identified the grass. Martin Püschel (AM) inked the drawings and photographed the shells, and Marlene Vial (AM) did the SEM work; the assistance of both of them is thankfully acknowledged. The authors thank John Stanisic and Winston Ponder for their comments on the manuscript for this paper. This project arose out of funding received from Natural Resource Management Board of the Northern Territory (Project number 2007083, to MFB) under the auspices of the Northern Territory Integrated Natural Resource Plan.

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Sepioloidea magna sp. nov.: a new bottletail squid (Cephalopoda : Sepiadariidae) from northern Australia

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ABSTRACT

Examination of specimens of *Sepioloidea* d'Orbigny, 1845, from northern Australia led to the discovery of a new species. It is described here as *Sepioloidea magna* sp. nov. It is distinguished from the other nominal *Sepioloidea* species, *S. lineolata* (Quoy & Gaimard, 1832) and *S. pacifica* (Kirk, 1882), by its size, number of tentacular club suckers, absence of obvious colour pattern and the modification of the hectocotylus.

KEYWORDS: Cephalopoda, Sepiadariidae, *Sepioloidea*, bottletail squid, Australia.

INTRODUCTION

A new species of sepiadariid (= bottletail) squid was discovered in the collection of the Museum and Art Gallery of the Northern Territory, Darwin, during a visit in 2008. It occurs in relatively deep water (225–300 m) in the Arafura Sea north of Darwin, Australia, and south of the eastern Indonesian island of Kep, Tanimbar Islands. It is assigned here to the genus *Sepioloidea* d'Orbigny, 1845, which presently contains only two species: *S. lineolata* (Quoy and Gaimard, 1832) and *S. pacifica* (Kirk, 1882). This new taxon is unusual among the Sepiadariidae Fischer, 1882 in being quite large, with one mature female examined here measuring 61.9 mm mantle length. In addition, other sepiadariids possess striking fixed colour patterns, a trait not seen in this species, which (in preserved specimens) appears dull in colour and not patterned.

Unfortunately the specimens are in less than perfect condition, typical of animals trawled from depth. Some features, such as the funnel organ, and features of the internal anatomy could not be seen clearly in any of the specimens examined so it cannot be fully described. However, this animal is so distinct from the other two representatives of the genus, that I have no hesitation in describing it as a new species.

MATERIALS AND METHODS

Terminology, measurements, indices, and abbreviations for anatomical structures follow Roper and Voss (1983), with a few minor differences (Table 1). In the current paper, ASC refers to the total number of suckers on each designated arm. This abbreviation refers to the number of suckers on the basal half of each arm in Roper and Voss (1983), with ASCT used there for the total number of arm suckers. As it is difficult to determine a reliable halfway measure, the utility of counting the suckers on the basal half of the arm only is dubious and is not used here. All measurements are in millimetres (mm).

Other abbreviations: MV – Museum Victoria, Melbourne; NTM – Museum and Art Gallery Northern Territory (formerly Northern Territory Museum), Darwin.

For scanning electron microscopy, arms and club suckers were removed, mounted, then air dried and examined in a JOEL JEM LA 6490 (Japan Electron Optics Ltd. Japan) scanning electron microscope operated at 15 kV.

TAXONOMY

Sepioloidea d'Orbigny, 1845

Gender feminine. Type species, by monotypy, *Sepiola lineolata* Quoy and Gaimard, 1832. Recent (temperate and tropical) Australia.

Diagnosis. Sepiadariid coleoids with body short; fins narrow, located medially on each side of body. Mantle fused with head in occipital area; mantle and funnel locking cartilage with 2 components. Arms joined by a wide web; web forms deep sheath around base of tentacles. Left ventral arm hectocotylised; suckers absent distally, pedicels modified forming series of transverse lamellae. Gladius absent. Light organs absent.

Sepioloidea magna sp. nov.

(Figs 1–7; Tables 1 and 2)

Material examined. HOLOTYPE – NTM P.41686, 1♂ (45.7 mm ML, possibly submature), Australia, Northern Territory, Arafura Sea, 82 nm due north of Cape Van Diemen, Melville Island, 9°47′S, 130°26′E, 225 m, coll. D. Evans on FV *Invincible*, 9 December 1990.

PARATYPES – NTM P.41641, 2♀ (60.0 mm ML, mature; 49.5 mm ML, submature), Northern Territory, Arafura Sea, 8°47′S 132°21′E, 274 m, coll. J. Todd on FV *Orion*,

Table 1. Description of measurements and counts. Definitions largely follow Roper and Voss (1983). New or modified definitions are indicated by an asterisk (*). Indices (shown in square brackets) are calculated by expressing each measure as a percentage of mantle length.

Arm Length – **AL**	length of each designated (i.e. 1, 2 etc.) arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [**ALI**].
Arm Sucker Count * – **ASC**	total number of suckers on each designated arm (e.g. ASC2).
Arm Sucker diameter – **AS**	diameter of largest normal sucker on each designated (i.e. 1, 2 etc.) arm [**ASIn**].
Club Length – **ClL**	length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [**ClLI**].
Club Row Count – **ClRC**	number of suckers in transverse rows on tentacular club.
Club Sucker diameter – **ClS**	diameter of largest sucker on tentacular club [**ClSI**].
Egg Diameter – **EgD**	diameter of largest egg present in the ovary or oviduct [**EgDI**].
Eye Diameter – **ED**	diameter of eye [**EDI**].
Fin Insertion – **FI**	length of fin as joined to mantle [**FII**].
Fin Insertion anterior * – **FIa**	anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [**FIIa**].
Fin Width – **FW**	greatest width of single fin [**FWI**].
Free Funnel length – **FFu**	the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [**FFuI**].
Funnel Length – **FuL**	the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral midline [**FuLI**].
Head Length – **HL**	dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [**HLI**].
Head Width – **HW**	greatest width of head at level of eyes [**HWI**].
Mantle Length – **ML**	dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle.
Mantle Width – **MW**	greatest straight-line ventral width of mantle [**MWI**].

4 June 1999; P.1387, 1♀ (55.9 mm ML, mature), Arafura Sea, north of Melville Island, 9°46′S, 130°14′E, 270–300 m, coll. Northern Territory Fisheries, 15 September 1987; NTM P. 41687, 5♀ (53.0, 58.7, 61.9 mm ML, mature; 35.5, 39.5 mm ML, submature), Arafura Sea, 82 nm due north of Cape Van Diemen, Melville, Island, 9°47′S, 130°26′E, 255 m, coll. D. Evans on FV *Invincible*, 9 December 1990.

Diagnosis. Mantle length in mature females up to approx. 60 mm. Colouration in preserved specimens bland, pale purplish grey, with tiny chromatophores (no stripes or spots). Hectocotylus structure: basal half of left ventral arm normal, distal half devoid of suckers, with approximately 22 rows of flap-like lappets that are bilobed dorsally, swollen in proximal 12 rows (approximately); ventral lappets consist of thin flaps joined distally to dorsal lappets. Tentacular club with approx. 40 transverse rows of minute suckers.

Description. Counts and indices for individual specimens are given in Table 2.

Species moderate size: ML male 45.7, females 39.5–<u>54.1</u>–61.9 (*SD*, 7.7; *n* = 7). Mantle short, broad, cylindrical in anterior half to two-thirds, rounded posteriorly; MWI male 81.0, females 75.0–<u>87.5</u>–96.7 (*SD*, 10.2; *n* = 6). Fins rather small, narrow, ear-like; fin length approximately 75% ML, FIIa male 20.6, females 22.5–<u>26.0</u>–29.9 (*SD*, 2.5; *n* = 6); fin width about 20% ML, FWI male 15.5, females 10.5–<u>18.0</u>–25.5 (*SD*, 5.6; *n* = 7), attached laterally between 1st and 4th quarters of mantle; posterior margins curved, tapered; anterior margins convex without well-developed lobes, lateral lobes crescentric. Anterior edges of fins do not project to level of anterior mantle margin (Fig. 1).

Funnel long, conical, base broad, tapered and projects anteriorly slightly beyond anterior margin of eye (Fig. 2A); FuLI male 53.6, females 48.5–<u>61.2</u>–72.7 (*SD*, 8.4; *n* = 7); free for most of its length, FFuI male 32.8, females 25.0–<u>28.4</u>–30.7 (*SD*, 2.6; *n* = 7). Funnel valve small, rounded anteriorly. Dorsal funnel organ structure not able to be determined (damaged in all specimens). Funnel locking cartilage with broad, deep anterior hollow and shallow, longer and narrower posterior groove. Mantle cartilage compliments funnel member with prominent anterior lobe and much smaller posterior lobe (Fig. 2B).

Head broader than long in both sexes, HLI male 70.9, females 55.4–<u>71.2</u>–89.6 (*SD*, 12.6; *n* = 7); HWI male, 72.6, females 56.5–<u>71.0</u>–80.0 (*SD*, 7.9; *n* = 7), narrower than mantle width. Eyes moderate in size, EDI male 17.7, females 13.1–<u>15.8</u>–20.2 (*SD*, 2.6; *n* = 7); ventral eyelids not free, eyes covered by transparent membrane; small olfactory pore present on latero-posterior surface of head, behind eye.

Arms robust, broad basally, tapered distally; order variable, arms 1 typically slightly shorter than other arm pairs (Table 2). Arm length index of longest arm in male (ALI3) 101.3, females (ALI3) 76.7–<u>87.1</u>–101.3 (*SD*, 9.0; *n* = 7). All arms similar in shape, semicircular to subtriangular in section; indistinct keels present on median aboral sides of arms. Sucker pedicels short, each with curved bilobed lappets on posterior margin. Arms suckers biserial proximally for about 10 rows, tetraserial distally; spherical throughout. Suckers on distal half of right ventral arm 4 of males, widely spaced, two rows on each side, arm fleshy medially. Largest arm suckers on each arm all of similar size. Suckers largest basally; smaller and crowded on distal arm

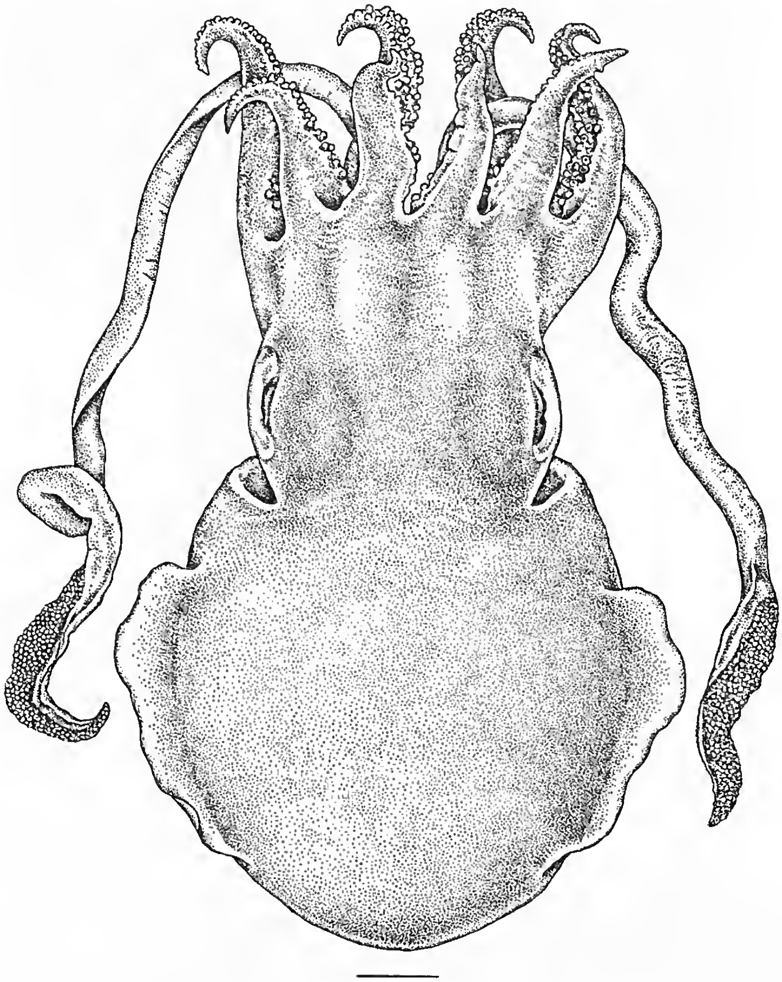

Fig. 1. *Sepioloidea magna* sp. nov.: dorsal view, female paratype, NTM P.41687, 53.0 mm ML, scale bar 10 mm.

tips. In male, basal 2–3 rows of suckers enlarged on arms 2 and 3 and to lesser extent on arm 4. Largest suckers on arms 4 smaller than those on arms 1. Suckers similar sized on all arms of females. Sucker counts range from 100–166 on each arm, mean sucker counts on arms 1–4 in females 119, 128, 143 and 141, respectively. All arms connected by relatively deep web, and bordered by shallow scalloped protective membranes.

Chitinous rims of all arm suckers with crenulated inner ring. Infundibulum with 7–10 rows of hexagonal processes with blunt pegs (Fig. 3A).

Left ventral arm of males hectocotylised. Suckers normal in size and shape; biserial arrangement basally for 12 rows, tetraserial for next 4–5 rows. Arm modified distally for approximately half its length; suckers absent, with 22 rows of flap-like biolobed lappets on dorsal side of arm. Dorsal lappets quite swollen for proximal 12 rows (approximately). Ventral lappets not bilobed, thin flaps joined distally to dorsal lappets. Deep furrow between dorsal and ventral lappets (Fig. 4A).

Tentacles long, slender, stalks naked, semicircular in section; oral surface convex. Club long (Fig. 4B), exceeds half mantle length ClLI male 54.7, females 58.2–66.0–75.1 (*SD*, 6.9; $n = 6$), not expanded, diameter uniform through most of length, tip tapers to blunt end distally. Suckers 0.15–0.20 mm diameter in centre of club; arranged in 39–42 oblique rows. Narrow swimming keel on aboral side of carpus extends posteriorly to slightly beyond carpus. Keel forms slight groove on oral side. Proximal third of keel widest.

Gills in all specimens in poor or damaged condition, hence number of lamellae per demibranch could not be determined.

Dentition of club suckers (Fig. 3B): inner ring with blunt teeth; teeth well defined on half of rim, rest indistinct. Infundibulum with round-ovate polygonal processes without pegs. At periphery, polygonal processes smaller, subrectangular.

Buccal membrane with 6 lappets; suckers absent. Females with deep buccal pouch on ventral side, formed from

Table 2. *Sepioloidea magna* sp. nov.: measurements (mm), counts and indices.

Museum Reg. no. Sex	NTM P.41686 holotype male	NTM P.41687 paratype female	NTM P.41641 paratype female	NTM P.41687 paratype female	NTM P.1387 paratype female	NTM P.41687 paratype female	NTM P.41641 paratype female	NTM P.41687 paratype female
ML	45.7	39.5	49.5	53.0	55.9	58.7	60.0	61.9
MWI	81.0	95.4	76.4	96.6	84.8	75.0	96.7	–
FWI	15.5	19.0	18.2	25.5	24.3	16.2	10.5	12.6
FIIa	20.6	26.6	26.3	24.5	29.9	22.5	–	26.2
FII	21.9	58.7	–	–	–	54.5	–	53.8
FuLI	53.6	67.1	72.7	60.4	53.1	59.6	66.7	48.5
FFuI	32.8	30.4	26.3	30.2	30.4	25.6	25.0	30.7
HLI	70.9	89.6	55.4	70.4	86.9	63.4	65.0	67.9
HWI	–	80.0	76.0	75.1	68.3	66.6	74.5	48.3
EDI	17.7	13.9	18.2	20.2	15.0	13.1	16.2	13.7
ALI1	65.6	78.5	78.8	75.5	71.6	69.8	80.0	74.3
ALI2	76.6	88.6	70.7	83.0	96.6	–	83.3	67.9
ALI3	78.8	101.3	88.9	96.2	85.9	76.7	80.0	80.8
ALI4	78.8	88.6	82.8	88.7	91.2	71.6	91.7	77.5
ASIn1	4.16	3.54	2.83	2.83	2.86	2.39	2.33	2.26
ASIn2	6.35	3.54	3.03	2.83	2.50	2.56	2.33	2.26
ASIn3	6.35	3.29	3.23	3.21	2.86	2.39	2.67	2.58
ASIn4	3.06	3.29	3.03	2.64	2.15	2.21	2.83	2.26
ASC1	76	116	126	128	134	100	118	112
ASC2	80	114	132	134	134	–	134	120
ASC3	100	140	143	152	152	130	144	138
ASC4	104	140	126	166	152	122	134	144
ClLI	54.7	63.3	60.6	73.6	75.1	–	65.0	58.2
ClRC	–	41	42	40	42	39	40	40
ClSI	–	0.51	0.40	0.38	0.36	0.34	0.25	0.32
EgDI	–	–	–	16.8	16.1	15.3	20.8	17.6

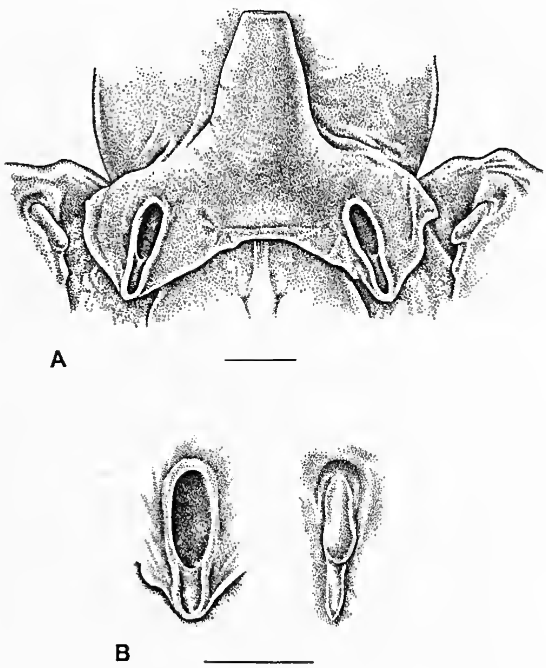

Fig. 2. *Sepioloidea magna*, sp. nov. **A**, funnel, female paratype, NTM P.41687, 53.0 mm ML, scale bar 10 mm; **B**, funnel locking cartilage (left) and mantle locking cartilage (right), same specimen, scale bar 10 mm.

expanded buccal membrane. Numerous spermatophores present in buccal pouch of all but smallest two specimens examined. Spermatophores also present attached to buccal mass in several specimens.

Upper and lower beaks (Fig. 5). Chitin, dark brown to black, darkens gradually from rostrum to hood, crest, and lateral walls. Upper beak with pointed, slightly curved rostral edge, jaw angle obtuse, lateral wall edge with shallow indentation; hood high above crest posteriorly, crest wide. Lower beak with almost curved rostral edge, rostrum slightly protruded, jaw angle obtuse, lateral wall edge without indentation, hood notch absent, wings almost straight, widely spread.

Radula with 7 transverse rows of teeth (Fig. 3C). Rhachidian teeth with very wide, narrow, rectangular bases, taper abruptly to single straight-sided, long, fine cusps. First lateral teeth, with much broader bases, differing markedly in outline to rhachidian teeth, with broad heel basally on outer side, narrower and pointed at base on inner side; teeth with short pointed cusps displaced laterally and directed towards midline of radula. Second and third laterals with elongate bases. Second laterals with narrow, rectangular bases, similar in shape to rhachidian teeth, cusps narrow, pointed, displaced toward midline of radula. Rhachidian, first and second lateral teeth strongly concave basally. Third laterals with sabre-like teeth, longer than second laterals.

Gladius absent.

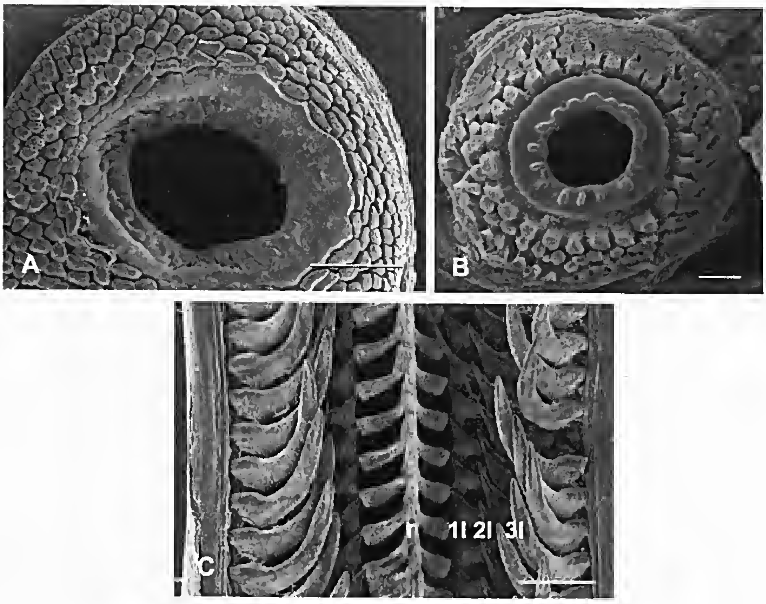

Fig. 3. *Sepioloidea magna*, sp. nov.: **A**, arm sucker rim, male holotype, NTM P.41686, 45.7 mm ML, scale bar 100 µm; **B**, tentacular club sucker, female paratype, NTM P.41687, 53.0 mm ML, scale bar 100 µm; **C**, radula, female paratype NTM P.1387, 55.9 mm ML, scale bar 200 µm. Abbreviations: r, rhachidian tooth; 1l, first lateral tooth; 2l, second lateral tooth; 3l, third lateral tooth.

The male reproductive tract was not removed from the only available male specimen because of its poor condition.

Female reproductive tract. Ovary large, occupies large proportion of posterior end of mantle cavity; displaces other organs when mature. Opens via single thick-walled oviduct at anterior end on left side. Nidamental glands paired, broad, located ventral to ovary toward anterior end. Inverted, cream coloured, U-shaped accessory nidamental glands located toward distal end of nidamental glands. Eggs spherical, 8.9–10.9 mm diameter; EgDI 15.3–17.3–20.8 (*SD*, 2.1; *n* = 5).

Colour in alcohol cream with tiny purple chromatophores peppered evenly over mantle, fins, head and arms; chromatophores on dorsal surface of mantle, fins and head slightly darker and more concentrated than those on ventral surface.

Type locality. Arafura Sea, due north of Cape Van Diemen, between northern Australia and Kep, Tanimbar (Indonesia), 9°47′S, 130°26′E, 225 m.

Distribution. Arafura Sea, from approx. 8°47′S, 132°21′E to 9°47′S, 130°26′E. Depth range 225–300 m (Fig. 6). (It is likely that MV specimens (identified as *Sepioloidea* and occurring at similar depths to those described above) from the Northwest Shelf, Scott Reef,

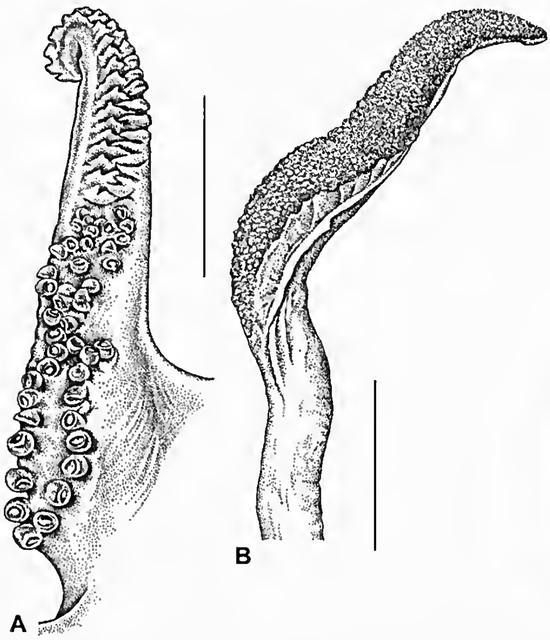

Fig. 4. *Sepioloidea magna*, sp. nov.: **A**, hectocotylus, male holotype, NTM P.41686, 45.7 mm ML, scale bar 10 mm; **B**, tentacular club, female paratype, NTM P.41687, 53.0 mm ML, scale bar 10 mm.

Fig. 5. *Sepioloidea magna*, sp. nov.: upper beak (left) and lower beak (right), female paratype NTM P.1387, 55.9 mm ML, scale bar 2 mm.

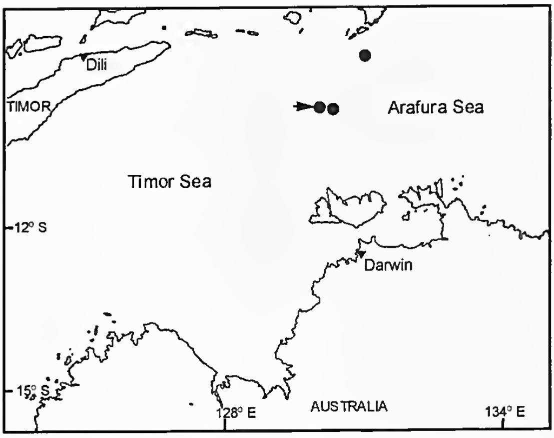

Fig. 6. *Sepioloidea magna* sp. nov. distribution. Arrow indicates the type locality.

and the Timor Sea: MV F.68177, 9°46′S, 130°17′E; MV F.68178, 18°48′S, 117°06′E; MV F.68179, 14°51′S, 121°35′E; MV F.68181, 18°29′S, 117°42′E, and MV F.68182, 18°25′S, 117°48′E, also belong to this species. However, I was not able to borrow this material. If these specimens are conspecific with this new species, its range actually extends westwards to the Timor Sea off Western Australia, to north of Dampier.)

Etymology. The species name, *magna*, is derived from the Latin, *magnus*, meaning large, or great and refers to the large size of this species compared to others in the genus. This specific name is adjectival in form.

DISCUSSION

The family Sepiadariidae was erected by Fischer (1882) to include two genera, *Sepiadarium* and *Sepioloidea*. *Sepiola lineolata* from Jervis Bay in NSW was described by Quoy and Gaimard in 1832 and later transferred to the genus *Sepioloidea* by d'Orbigny (1845). The history of the definition of the family and its genera was reviewed in detail by Berry (1921). Over the years there have been many generic-level reclassifications and uncertainties, many of which remain.

Sepioloidea lineolata is widespread in Australian waters, occurring in shallow water around the southern Australian coastline. The distinct patterning of this small 'Striped Pyjama Squid' (Norman and Reid 2000) has meant that any specimens of this taxon that are collected are typically identified as *S. lineolata*. However, they need to be critically re-examined to determine whether all representatives do, in fact, belong to a single species.

Sepioloidea pacifica was described by Kirk in 1882 (again initially placed in the genus *Sepiola*) based on a specimen collected in Wellington Harbour. The original description is very brief and the type specimen has been lost. Dell (1952: 87) comprehensively redescribed the supposed species, but qualified his description by saying: "There is no complete certainty that the species here described is conspecific with Kirk's *Sepiola pacifica*, but the writer has seen no other Cephalopod from New Zealand which approaches this species". The specimens Dell examined (56 males, and one female) were from Lyttelton Harbour and not the type locality, hence, he did not establish a neotype in that publication. Following the collection of additional specimens from the type locality, he did so a few years later (Dell 1959: 2).

Sepioloidea pacifica is now known to be widespread in New Zealand waters and has been collected from depths ranging from approx. 15–550 m from the following additional locations: *North Island*, off Tryphena, Great Barrier Island, Cape Colville, Hauraki Gulf, Hawkes Bay, Lowry Bay and Cook Strait and the *South Island*, off Cape Campbell, Middle Bank, Kaikoura, Dunedin Harbour, Mernoo Bank, the Chatham Rise, Chatham Islands and Waitangi (Powell 1979). It has also been reported from the Nazca and Sala y Gómez submarine ridges in the eastern Pacific Ocean (Parin *et al.* 1997), although these locality records in the eastern Pacific require additional verification.

Sepioloidea lineolata differs from *S. pacifica* based on the presence of: a fringed dorsal anterior margin (lateral to the junction of mantle and head); numerous cuticular pores on the sides and ventral surface of the head and mantle, and in the presence of longitudinal stripes on the dorsal side of the body, head and arms. In *S. pacifica* the mantle is not fringed, and the body pigment consists of numerous, small, dark chromatophores.

Sepioloidea magna differs from its congeners in a number of traits. *Sepioloidea lineolata* is very distinctive in having a fringed anterior mantle margin adjacent to the junction of the dorsal mantle and the head. In addition, the sides and ventral surface of the head and mantle are covered with numerous tubercles (openings of cuticular pores), from which copious quantities of slime are released when these animals are attacked or disturbed (Norman 2000). The dorsal side of the body, head and arms is banded with brownish stripes – the dramatic patterning perhaps indicative of toxicity. The club of *S. lineolata* has suckers arranged in 20 rows, while in *S. magna* the suckers are minute and arranged in approximately 40 rows.

Sepioloidea pacifica is similar to *S. magna* in that it does not have a fringed mantle margin. It has a smooth body surface without tubercles. However, the body in *S. pacifica* is covered with numerous, small, dark chromatophores and is dark purplish to black in colour, unlike that of *S. magna*. The arms suckers are biserial in *S. pacifica* rather than tetraserial over a portion of the arms as in *S. magna*. The club of *S. pacifica* has suckers arranged in four rows. The modification of the hectocotylus also appears to differ. As described by Dell (1952: 82): "Paired furrows set somewhat obliquely render this portion of the arm rather feather-like. A deep longitudinal groove runs along the left margin". No such groove can be seen on the modified portion of the

arm in *S. magna* and the modification of the lappets is quite different as can be seen by comparing Fig. 4A and Fig. 7 (redrawn from Dell (1952)).

Sepioloidea magna is the largest of the three nominal species of the genus that are now known. The holotype (45.7 mm ML) did not contain spermatophores, but it is difficult determine whether the animal is mature or may have spent the spermatophores prior to capture. The smallest mature female (i.e., containing well developed ovarian eggs) was 53.0 mm ML (Table 2).

It remains to be seen whether the Sepiadariidae represents a monophyletic group. Phylogenetic analysis of the cephalopods in general and members of the Sepioidea in particular is limited in its scope and most analyses include only a limited number of taxa. A comprehensive revision all genera within the Sepioidea is long overdue.

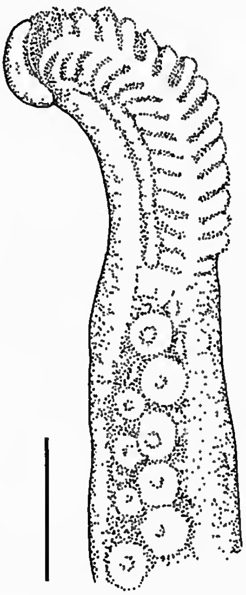

Fig. 7. *Sepioloidea pacifica* hectocotylus (redrawn from Dell 1952, Pl. 34, fig. 4), scale bar 2 mm.

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Distribution and habitat use by *Hemidactylus frenatus* Duméril and Bibron (Gekkonidae) in the Northern Territory, Australia

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ABSTRACT

Hemidactylus frenatus is an invasive gecko with an expanding distribution in Australia. We collated all available locality records and investigated the habitats associated with the species in the Northern Territory. *H. frenatus* is more widespread in the Top End, Gulf of Carpentaria and Victoria River regions than previously documented. The species remains primarily associated with artificial anthropogenic structures and surrounding vegetation (particularly denser tropical forests), but there are also a small number of records of it living in natural vegetation further than 1 km from such structures. We speculate that *H. frenatus* will continue to spread through suitable habitats in northern Australia.

KEYWORDS: *Hemidactylus*, Gekkonidae, invasive species, Northern Territory.

INTRODUCTION

The Asian House Gecko, *Hemidactylus frenatus* (Fig. 1), is presently widespread in tropical and sub-tropical regions throughout the world, occurring in Asia (Manthey and Grossman 1997; Goris and Maeda 2004), Australasia (Cogger 2000), the Pacific (Case *et al.* 1994), the Americas (Savage 2002; Schmidt Ballardo *et al.*1996; Townsend and Krysko 2003; Rivas Fuenmayor *et al.* 2005), Africa and Madagascar (Spawls *et al.* 2001) and the Mascarene Islands (Cole *et al.* 2005). The species is introduced within most of its range and its origins are obscure, but they probably lie within south-east Asia. Where introduced, *H. frenatus* is normally associated with human dwellings or other structures (e.g. Galina-Tessaro *et al.* 1999; Lee 2000; McCoy 2000; Goris and Maeda 2004).

In Australia, *Hemidactylus frenatus* occurs in coastal Queensland, northern coastal New South Wales, the Northern Territory from the coast south along the Stuart Highway to 22°S, and also in scattered locations in the Pilbara and Kimberley, north-western Western Australia (Cook 1990; Wilson and Swan 2008). Typically, the species is described as almost completely confined to artificial habitats associated with humans, including derelict buildings, rubbish heaps and vehicles (Wilson and Knowles 1998; Wilson 2005). Cogger (2000) suggests "a dependance on man for its distribution in this country", and in Brisbane, south-east Queensland, this remains the case according to literature (Keim 2002; Newbery and Jones 2007). However, elsewhere in the country there are published records of *H. frenatus* in habitats away from human habitation. In the Northern Territory, as early as 1980 its presence was noted in coastal monsoon forest and mangrove at Buffalo Creek, north-east of Darwin (Kikkawa and Monteith 1980), and Keim (2002) records established populations in bushland adjacent to Darwin. Gambold and Woinarski (1993) documented further records in monsoon forest patches at Gunn Point, north-east of Darwin, and in the Daly River area. In Queensland, *H. frenatus* has recently been recorded in coastal *Casuarina* forest and adjacent littoral vine scrub on the western coast of Cape York Peninsula, approximately 100 km south of Weipa (Clarke 2006). In contrast, surveys in the immediate vicinity of Weipa (Winter and Atherton 1985), and of monsoon forests in the Kimberley, Western Australia (Kendrick and Rolfe 1991), did not find the species.

The colonisation of new areas around the world by *Hemidactylus frenatus* and its effect on indigenous gecko taxa have been the subject of much interest. A number of gecko species are known to have suffered a negative impact from it. On the Mascarene Islands for example, *H. frenatus* most likely caused the extinction of some indigenous *Nactus* spp. by outcompeting them for use of refugia and through predation and other agonistic behaviour (Cole *et al.* 2005). On some Pacific islands *H. frenatus* has replaced *Lepidodactylus lugubris* as the dominant gecko on artificial structures (Case *et al.* 1994); in Hawaii the primary mechanism for this domination is the superior foraging ability in *H. frenatus*, rather than agonistic interactions (Petren and Case 1996). Rivas Fuenmayor *et al.* (2005) suggest *H. frenatus* has caused declines of *Gonatodes albogularis* and *Phyllodactylus ventralis* in Venezuela.

A number of Australian gekkonid taxa may be impacted by the invasion of *Hemidactylus frenatus*. *Gehyra australis* and *G. dubia* are common inhabitants of anthropogenic structures (Wilson and Swan 2008). Species of both

Fig. 1. Live *Hemidactylus frenatus*, *in situ* at night, Nightcliff, Darwin, Northern Territory, 10 October 2009. **A**, In its usual hunting pose on a fly screen inside a house; **B**, on base of trunk of a *Carpentaria acuminata* palm outside a house. Photos. J. Lindley McKay.

Nactus and *Lepidodactylus*, genera in which declines are documented elsewhere, occur in Queensland on man-made structures and in closed forests. Like other affected taxa, *Lepidodactylus pumilus* is restricted to an island distribution. The impact of *H. frenatus* on these geckos and other components of Australian ecosystems are yet to be documented.

Given the potential for impact on indigenous gecko species, it is desirable to investigate the ecology of *H. frenatus* in Australia. In this study the geographic focus was limited to the Northern Territory of northern Australia. We addressed the following questions: What is the current geographical range of *H. frenatus* in the Northern Territory, and with which habitat(s) is *H. frenatus* currently associated in the Northern Territory?

METHODS

Assessing current range. The current range of *Hemidactylus frenatus* in the Northern Territory was assessed using two sources of data – the Northern Territory Vertebrate Fauna Atlas (NTVFA) and field surveys. The NTVFA is a database maintained by the Biodiversity Conservation unit of the Northern Territory Department of Natural Resources, Environment, the Arts and Sport (NRETAS) which holds geolocated fauna records from an array of sources including CSIRO, the Northern Territory Biological Records Scheme, Australian museums, Australian universities, peer-reviewed literature, environmental literature (e.g. environmental impact assessments), and non-government organisations such as Birds Australia. The NTVFA contains 185 records of *Hemidactylus frenatus* between 20 February 1937 and 21 August 2001 and lists the location, date, and organisation that collected the information.

Field surveys were conducted from 23 July 2002 to 4 September 2005, in parts of the Top End of the Northern Territory north of 15° S and the Gulf of Carpentaria region. Information collected included date, location and habitat. Where possible, surveys were conducted from dusk until the third hour after sunset, as *H. frenatus* has been noted to be most active in the earlier hours of the night (Frankenberg and Werner 1981). Surveys were usually limited to 10 minutes. Identification could be made reliably and with ease as *H. frenatus* is the only gecko species with a multiple chirp call throughout most of the Northern Territory, and

in the localities where *Lepidodactylus lugubris* also occurs (Woinarski *et al.* 1999, McKay and Horner 2007), identification of *H. frenatus* can be made visually by observing the rows of spines on the dorsal surface of the tail (Fig. 1).

The combined data spanned 68 years from 1937 to 2005. All localities were combined using GIS to identify the current known Northern Territory distribution.

Assessing current habitat associations. To assess habitats associated with *Hemidactylus frenatus* we used field survey data, and any habitat information attached to the NTVFA records. During field surveys we collected the following information: date, location, distance to nearest vehicle access or artificial structure, and habitat type (i.e. artificial structure, coastal monsoon forest, riparian monsoon forest, riparian forest, eucalypt woodland, *Melaleuca* swamp forest, coastal *Casuarina* forest, mangrove, campground or open area). Habitats were classified into four categories: (1) structures (including disused vehicles and building ruins); (2) naturally occurring vegetation 0–500 m from the nearest vehicle access or artificial structure; (3) naturally occurring vegetation 500–1000 m from the nearest vehicle access or artificial structure; and (4) naturally occurring vegetation >1000 m from the nearest vehicle access or artificial structure.

The greatest portion of NTVFA records had no attached habitat data. Those that did provided various information including canopy height, canopy cover percentage and a general site description.

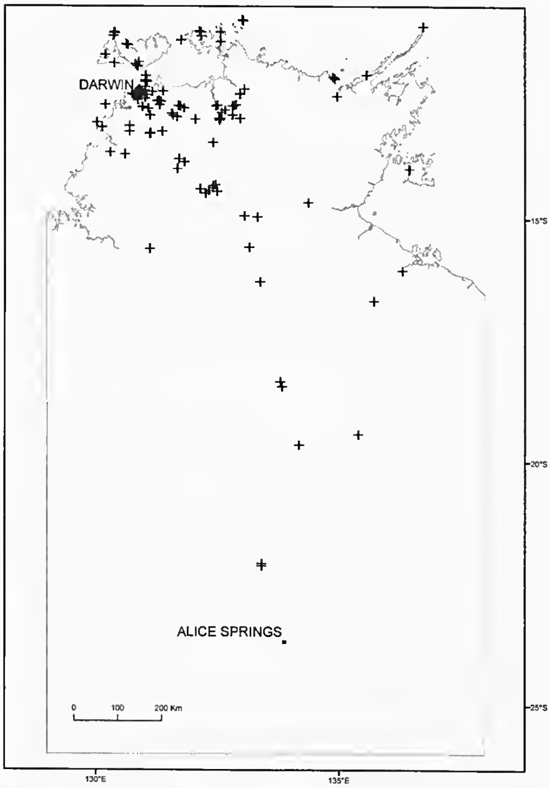

Fig. 2. Current distribution of *Hemidactylus frenatus* in the Northern Territory, from the combined records of the Northern Territory Vertebrate Fauna Atlas and field surveys.

RESULTS

Current range. Based on NTVFA and field survey data, *Hemidactylus frenatus* is currently confined to areas north of the Tropic of Capricorn in the Northern Territory, and is most densely represented by localities in the north-western Top End (Fig. 2). There are scattered records throughout other parts of the Top End, including coastal Arnhem Land, and the Tiwi, Croker, Marchinbar and Groote islands. South of 15°S localities become sparser, with records along the Stuart Highway, three records from the Gulf country and one from the Victoria River District. South of 17°S *H. frenatus* is confined to localities on the Stuart and Barkly Highways, and there are no records south of Ti Tree at 22°S.

Current habitat associations. Based on the field survey data, *Hemidactylus frenatus* utilises both artificial structures and natural habitats in the Northern Territory (Table 1). Most records from artificial structures are within the region of highest regional abundance (the western Top End), which is also the region with the largest infrastructure and human population. One record provided the second locality at which artificial structures are used in the sparsely populated Gulf of Carpentaria region.

In field surveys, *Hemidactylus frenatus* was recorded from riparian vegetation (n=8), eucalypt woodland (n=4), coastal monsoon forest (n=3), riparian monsoon forest (n=3), *Melaleuca* swamp forest (n=1), and coastal *Casuarina* forest (n=1). Of the 18 total locations where *H. frenatus* occupied natural habitats, 13 represented records within 500 m of structures or vehicle access. *Hemidactylus frenatus* occurred up to 1 km from a structure or vehicle access at two localities in the Darwin area, in coastal monsoon forest and *Melaleuca* swamp forest habitats. Records from greater than 1 km from a structure or vehicle access occurred in both the Darwin area (two localities, in coastal monsoon forest and coastal *Casuarina* forest) and Kakadu National Park (one locality, in riparian monsoon forest).

Twenty site records from the NTVFA also included data on habitat association for *H. frenatus*. Habitats were monsoon forest (n=15), woodland (n=3), woodland on foreshore (n=1), and floodplain edge with scattered low trees (n=1). The monsoon forests had canopy heights of between 7 and 20 m, and canopy covers of between 20 and 90%. Woodlands had canopy heights of 9–12 m, and canopy covers of 8–40%.

Neither field surveys nor the NTVFA provided any records from natural habitats south of 15°S.

Table 1. Habitat associations of *Hemidactylus frenatus* in the Northern Territory, from field survey records. Abbreviations: **DVA** = distance from vehicle access or artificial structure; **KNP** = Kakadu National Park.

Date	Location	Latitude, Longitude	Habitat	DVA 0–500 m	DVA 500–1000 m	DVA >1000 m
23/07/02	East Point Recreation Reserve, Darwin	12°24′43.8″S, 130°49′24.2″E	Monsoon forest	X	X	
29/12/02	Walker Creek, Litchfield National Park	13°05′10.6″S, 130°41′57.8″E	Riparian vegetation	X		
07/02/04	Mataranka Hot Springs	14°57′29.8″S, 133°19′56.2″E	Riparian forest	X		
24/03/04	Casuarina Coastal Reserve, Free Beach carpark to Lee Point	12°21′46.7″S, 130°52′02.2″E to 12°19′55.1″S, 130°53′42.9″E	Coastal monsoon forest dominated by large *Acacia auriculiformis* and coastal *Casuarina* forest dominated by *Casuarina equisetifolia*	X	X	X
14/05/04	Fogg Dam	12°34′48.5″S, 131°20′23.6″E	Riparian vegetation dominated by *Acacia auriculiformis*	X		
05/08/04	Gunlom, KNP	13°26′00.8″S, 132°24′54.6″E	Riparian vegetation	X		
22/08/04	South Alligator river, KNP	12°39′29″S, 132°30′19″E	riparian strip along river bank	X		
22/08/04	Aurora South Alligator resort campground, KNP	12°40′29″S, 132°28′47″E	Artificial structure			
23/08/04	East Alligator Day Use area, KNP	12°25′23.8″S, 132°57′′57.9″E	Riparian forest	X		
23/08/04	Manngarre Walk, KNP	12°25′15.0″S, 132°58′01.4″E	Riparian monsoon forest	X	X	X
25/08/04	Nourlangie, KNP	12°51′51.7″S, 132°48′53.5″E	Eucalypt woodland dominated by *Eucalyptus miniata*	X		
25/08/04	Jabiru	12°40′31″S, 132°50′09″E	Artificial structure			
26/08/04	Jim Jim billabong campground, KNP	12°56′30.9″S, 132°33′13.9″E	Woodland adjacent to riparian zone	X		
29/08/04	Nitmiluk National Park	14°19′08″S 132°25′17″E	Large dense trees in the campground	X		
05/09/04	Mandorah	12°25′59″S 130°45′46″E	Artificial structure			
18/11/04	Hyptis Heights, KNP	12°48′48.5″S, 132°35′40.1″E	Artificial structure			
01/12/04	Jim Jim ranger station, KNP	12°55′48.1″S, 132°34′08.5″E	Artificial structure			
06/12/04	Mardugal campground, KNP	12°55′55.8″S, 132°32′19.1″E	Woodland and riparian vegetation, dominant trees include *Acacia auriculiformis* and *Pandanus spiralis*	X		
11/12/04	Holmes Jungle Nature Reserve, Darwin	12°24′06.5″S 130°55′53.6″E	Monsoon and *Melaleuca* swamp forest	X	X	
14/12/04	Nourlangie Camp, KNP	12°45′42.7″S, 132°39′37.9″E	Monsoon forest	X		
16/12/04	Bowali Visitor Centre, KNP	12°40′32″S 132°49′02″E	Artificial structure			
16/12/04	Bark Hut (Annaburroo)	12°54′00.7″S, 131°40′32.4″E	Artificial structure			
22/12/04	Manton Dam	12°51′44.0″S, 131°07′01.4″E	Riparian forest dominated by *Acacia auriculiformis* and *Melaleuca*	X		
23/12/04	Bardedjilidji walk, KNP	12°25′58.5″S, 132°58′11.2″E	Woodland dominated by *Eucalyptus* spp. and *Pandanus spiralis*	X		
08/05/05	Cape Crawford	16°41′01.7″S, 135°43′30.5″E	Artificial structure			
20/08/05	Gunbalanya (Oenpelli)	12°19′35.9″S 133°03′21.5″E	Artificial structure			
04/09/05	Gunn Point	12°09′33.4″S 131°01′16.2″E	Coastal monsoon forest, largest trees *Bombax ceiba* and *Acacia auriculiformis*	X	X	X

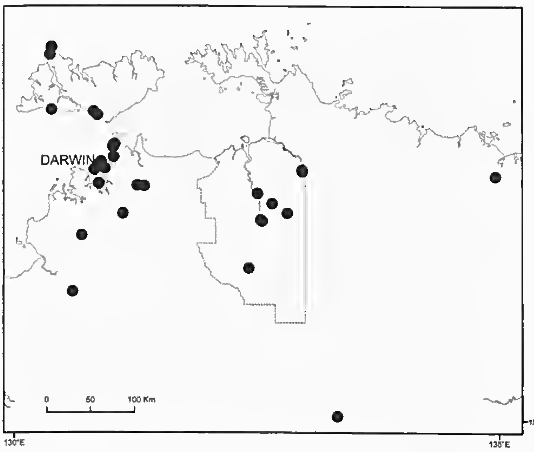

Fig. 3. Distribution of *Hemidactylus frenatus* in natural habitats in the north-east and central-north of the Northern Territory, Australia, from the combined records of the Northern Territory Vertebrate Fauna Atlas and field surveys. Dashed line indicates the border of Kakadu National Park.

DISCUSSION

The collation of site records clearly shows that *Hemidactylus frenatus* is established in many areas of the tropical Northern Territory, in particular the Top End north of 16°S, although some records may represent temporary introductions. Recent literature (e.g. Cogger 2000) portrays a distribution confined to localities along the Stuart Highway – essentially a strip down the centre of the Northern Territory. But here we show that *H. frenatus* is present to the east and to the west of the Stuart Highway, with many localities broadly distributed north of 16°S, and more sparsely separated localities further south. Both this study and previous literature indicate a southerly range limit of 22° S. Ota (1994) found that eggs of *H. frenatus* would not hatch below 19° C, and this is probably one factor limiting the southerly distribution.

Habitat association data presented here show *Hemidactylus frenatus* utilising both artificial and natural habitats (Table 1). Much recent literature has regarded the species as dependant on artificial habitats (e.g. Cogger 2000, Wilson 2005) and overlooked or ignored the few documentations of natural habitat use (Kikkawa and Monteith 1980; Gambold and Woinarski 1993; Keim 2002). From this study it can be seen that *H. frenatus* commonly occurs in natural vegetation proximate to human habitation or vehicle access in the Northern Territory north of 15°S (Fig. 3). The most frequently recorded of these natural habitats were forests with comparatively dense canopies or eucalypt woodland adjacent to closed forests. These types of forests possibly provide a preferable thermal range for a species adapted to mesic tropical conditions. Alternatively, tree species associated with denser forests may provide more suitable refugia for the colonisers than the smooth-barked eucalypts that predominate in open woodland. In the one woodland site not adjacent to denser forest where *H. frenatus* was recorded (Nourlangie carpark, Kakadu National Park), repeat surveys in 2004 did not record the species, and we suspect that the population has not persisted there. Although data do not show the habitat association for records south of 16°S, the distribution along major highways suggests that with the lack of mesic vegetation the species is more likely to be restricted to artificial structures in this part of the Northern Territory.

It is probable that our data underestimates the distribution of the species in natural habitats, as we are aware that some NTFVA sites, although having no data attached, are from natural habitats. One area for which this is the case is the coast of the Cobourg Peninsula (J. Woinarski pers. comm.). One specimen was collected at Port Essington by John Gilbert between 1838 and 1841 (Fisher and Calaby 2009), but the habitat was not recorded [Incidentally there was no sign of the species there during CSIRO visits between 1966 and 1969 (Fisher and Calaby 2009).] These sites, on the extreme north of Australia's coast, may represent the oldest sites of colonisation by this gecko in the country. *Hemidactylus frenatus* has occurred in the Northern Territory since at least the 1800's (Cogger and Lindner 1974), however trepang fishers from Sulawesi, Timor and New Guinea (popularly known as Macassans) regularly visited northern Australia from as far back as 100 years before European settlement (Macknight 1976), and the Cobourg Peninsula was a well-known destination of these traders (see Mitchell 1995).

Many features of the biology of *Hemidactylus frenatus* make this gecko well suited for colonisation, such as the ability of females to store sperm for up to 36 weeks (Murphy-Walker and Haley 1996), the ability to outcompete other geckos without costly agonistic interactions (Petren and Case 1996), and the ability to use its own species as a food source (Galina-Tessaro *et al.* 1999). Given these findings, it seems probable that *H. frenatus* will colonise suitable artificial anthropogenic and natural habitats throughout tropical Australia. We are aware of a number of undocumented populations in Arnhem Land (P. Horner pers. comm.) and inland Queensland (JLM unpub. data). Further study of *H. frenatus* provides numerous opportunities for research into both theoretical issues, such as the mechanisms of competition, and applied management issues, such as the anthropogenic means of dispersal in invasive species.

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Short Communication

Anadara granosa (Mollusca: Bivalvia: Arcidae) discovered live in Darwin Harbour, with implications for understanding climate change in northern Australia

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In August 2008, sampling of mudflats on the southern shoreline of Middle Arm peninsula, Darwin Harbour, located an extant population of *Anadara granosa* (Linné), a bivalve mollusc commonly called Roughback Cockle [the FAO name is Granular Ark]. This species occurs in huge quantities in prehistoric shell middens around Darwin, but is now very rare and was thought to be possibly locally extinct. The discovery came out of the need to locate live specimens for comparison with archaeological shells submitted for isotope analysis as part of a larger project 'Climate Change and Human Behavioural Variability in the Coastal Wet-Dry Tropics of Northern Australia'. This collaborative project, being lead by Dr Sally Brockwell of the Australian National University, seeks to explore links between climatic/environmental/ecological/malacological change and the interpretations of major cultural change in the archaeological record in three geographically distinct coastal regions of tropical northern Australia.

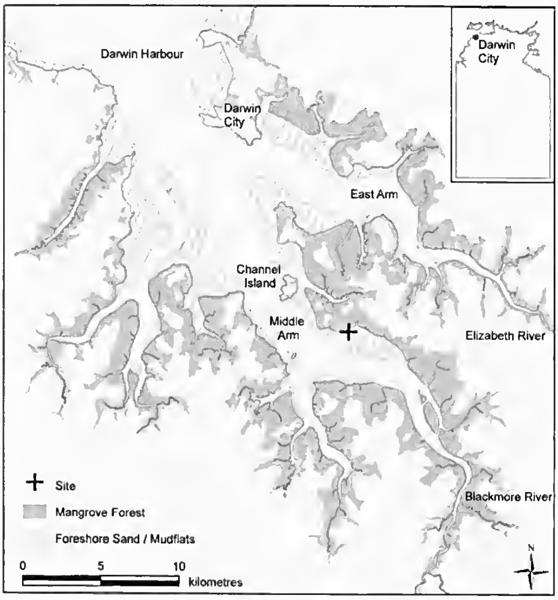

Fig. 1. Location of sampling site, Middle Arm peninsula, Darwin Harbour, Northern Territory. Illustration courtesy M. Fegan.

The site at which the *Anadara granosa* (hereafter *Anadara*) were located is on the shoreline of Middle Arm, the largest sub-estuary of Darwin Harbour (Fig. 1), fed mainly by the Blackmore River with freshwater flows during the wet season. This site, in an embayment on the Middle Arm mainland downstream of Channel Island, was chosen because of the relatively easy access to mudflats close to existing Aboriginal shell middens that are dominated by *Anadara* shells. These tidal mudflats are mainly formed from intertidal marine alluvium, mud, clay and silt (Pietsch 1986; Michie 1988).

Access to the site was gained through the wide mangrove forest that today fringes much of the Harbour (Brocklehurst and Edmeades 1996) via a low rocky ridge extending to an oyster-dominated (*Saccostrea cucullata* (Born)) reef at the seaward edge. The main mangrove species observed on this tidal mudflat are *Rhizophora stylosa* Griff. in the central zone and *Sonneratia alba* Smith in A. Rees on the seaward fringe. The area is generally undeveloped, apart from an aquaculture farm that presently operates some two kilometres south of this site.

The site was sampled on 5 and 22 August 2008, in the second half of the seven month long dry season that characterises Darwin's monsoonal climate. Sampling on both occasions was conducted over an area of approximately 10 m^2 and over approximately 1.5 hr on a spring low tide (Fig. 2). One adult *Anadara* (shell length 36.1 mm) was found live on the first occasion (Fig. 3). On the second occasion, four live adults (shell lengths 47.3, 43.6, 39.0, 51.6 mm) and one freshly dead *Anadara* with conjoined valves (shell length 49.8 mm) were found. Of this total of six live/fresh *Anadara*, three were located at the surface and three were buried 6–10 cm down in very soft fine black silty mud that was 80–90 cm deep and contained abundant disarticulated dead valves of *Anadara* and *Placuna placenta*.

Fig. 2. M. Fegan thigh-deep in mud at sampling site. Note pneumatophores of *Sonneratia alba* in foreground. Photo. R.C. Willan.

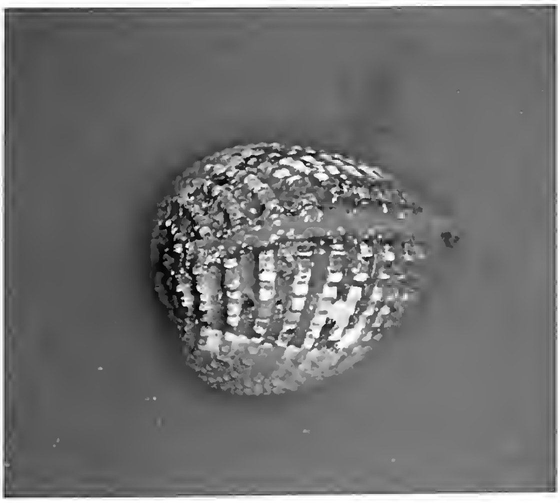

Fig. 3. Ventral view of live *Anadara granosa* individual (NTM P.41871) photographed soon after collection. Photo. R.C. Willan.

When collected, and immediately thereafter, the *Anadara* were crawling very actively, indicating the probability of considerable movement within the substrate when alive. Following fixation in absolute ethanol enabling future genetic analyses, all the animals were dissected from their shells and deposited in the mollusc collection of the Museum and Art Gallery Northern Territory under the registration numbers P.41871 (for the specimen collected on 5 August) and P.41930 (for the specimens collected on 22 August). The shells themselves were then sent overseas for isotope analyses. The results of this analysis will be compared with the results of isotope analysis of archaeological *Anadara* shells sampled from radiocarbon-dated shell mounds during excavations in 1996 on the same section of southern shoreline of Middle Arm peninsula and from Hope Inlet, Shoal Bay.

Since no study has been conducted on the growth of *Anadara* in northern Australia we do not know precisely how old these individuals from Darwin Harbour might be. In India, Narasimhan (1968) reported that *Anadara* reaches 31.5 mm shell length after one year, 49.5 mm after two years, and attains sexual maturity at seven months old.

Valves of *Anadara* dominate prehistoric shell mounds around Darwin Harbour (Fig. 4), suggesting large populations once existed that must have been easily exploited by the local inhabitants. All *Anadara*-dominated mounds that have been radiocarbon dated thus far belong to the pre-European period, formed mainly between 1500 and 500 years BP (Bourke 2004; Bourke and Crassweller 2006). *Anadara*, whose preferred habitat is mudflats in protected bays and estuaries (Poutiers 1998; R.C. Willan pers. obs.), no longer occurs in any significant quantity in the Darwin coastal environment of extensive mangrove-colonised tidal flats, suggesting extirpation through local environmental change (Hiscock 1997). Cessation of the *Anadara* mound building period across the northern Australian coast by 500 years BP also suggests regional climatic/environmental change (Bourke *et al.* 2007). While it may have declined in abundance, people continued to harvest *Anadara* after the mound-building period ceased. Local Aboriginal people in the Darwin area report that when they were children (some 30–40 years ago) they knew of areas supporting enough *Anadara* to collect a couple of buckets (Bill Risk pers. comm.), but that even this quantity has declined in recent years.

By contrast, today the most common edible molluscs associated with mangroves in Darwin Harbour are the gastropods *Telescopium telescopium* (Linné) (family Potamididae), *Terebralia* spp. (family Potamididae) and *Nerita balteata* Reeve (previously known as *N. lineata* Gmelin, but this name is preoccupied) (family Neritidae) (Smith *et al.* 1997; Bourke and Willan pers. obs.). These gastropods occur only in small numbers in the shell mounds around Darwin. Significantly, these species of molluscs, together with others – of Potamididae and Ellobiidae, and bivalves of the family Corbiculidae – that occur sympatrically with them, are euryhaline and much more tolerant of long temporal extremes and wide fluctuations in salinity and temperature than stenohaline mudflat bivalves such as *Anadara* (Healy and Wells 1998; Peterson and Wells 1998; R.C. Willan pers. obs.).

While *Anadara* is known to tolerate a range of physical environmental factors, proliferation to abundance does require an optimal habitat setting. Shore elevation, slope of the seabed and substrate type are some known factors that affect successful *Anadara* recruitment, growth and population stability (Broom 1985). Studies elsewhere in the Indo-Pacific have established that the highest population densities of *Anadara* occur in the fine soft brackish muds of open intertidal mudflats bordering, but not within, mangrove swamps and near, but not in, the mouths of large rivers (Broom 1982, 1985; Pathansali 1966). These habitats provide the optimal conditions of soft brackish (salinity between 26 to 31 ppt) fine silt-mud substrate, intertidal or marginally subtidal elevation level with a particular slope of seabed, and

Fig. 4. Typical *Anadara*-dominated prehistoric shell midden on Middle Arm peninsula coast near sampling site. Photo P.M. Bourke.

temperature of 25 to 32°C (Broom 1982:136–7; Pathansali 1966:91). Broom (1982: 137–138) noted that in *Anadara* beds on Malaysian mudflats there was a black sulphide-rich layer 3–4 cm below the surface, and comments that sandier substrates represent a suboptimal habitat for this species.

Of particular interest to us is the distinct difference between the habitat of the modern *Anadara* reported here for Darwin Harbour and that reported for *Anadara* collected by the Anbarra people of the Blyth River area of central Arnhem Land in the 1970s. As noted above, the fine silty black mud of these Middle Arm mudflats is 80–90 cm deep. Collection of the five live *Anadara* was extremely difficult and physically exhausting in this habitat, requiring ploughing through thigh-high mud (Fig. 2) for over two hours. This is in sharp contrast to the Blyth River habitat, where *Anadara* is collected from much sandier mudflats: "gatherers remain upright and mobile, moving over large areas during one session" … and … "Groups of women and children … rove slowly over the area containing *A. granosa*, pausing to dig out a shell, when one is sighted, with their fingers, a digging stick or a file". In 80 minutes on 16 August 1972, 37 kg of *Anadara* (approximately 1000 individuals) were collected by this method (Meehan 1982: 97).

It is known that *Anadara* can recruit to a range of (muddy to muddy-sandy) substrates in sheltered habitats, but it appears that peak settlement – or peak survivorship – only occurs on muddy sand flats that fall within a restricted range of silt/clay fraction/particle size of the substrate (cf. Broom 1985: 5). More research is needed to explore the role played by other factors in the decline of *Anadara* in this region, such as possible increasing extremes in range of salinity and temperature conditions.

Our observations of low densities of living *Anadara* are in accord with evidence for ongoing progradation of mudflats and subsequent colonisation by mangroves in the Darwin region (Woodroffe and Grime 1999: 319). In fact, the specimens we collected may be existing/surviving in a suboptimal habitat in the face of an accreting shoreline and seaward mangrove growth, as has been observed to rapidly encroach on *Anadara* culture sites on a Malaysian foreshore (Macintosh 1982: 13).

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We are particularly grateful to Matthew Fegan (Biodiversity Group, Department of Natural Resources, Environment, the Arts and Sport) for venturing into, and wading through, thigh-deep mud to collect these specimens for us, and also for preparing Fig. 1. Bill Risk kindly shared his recollections of the occurrence of *Anadara* in times gone by with us.

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Short Communication

Rectification of the type status for *Philiris ziska titeus* D'Abrera, 1971 (Lepidoptera: Lycaenidae)

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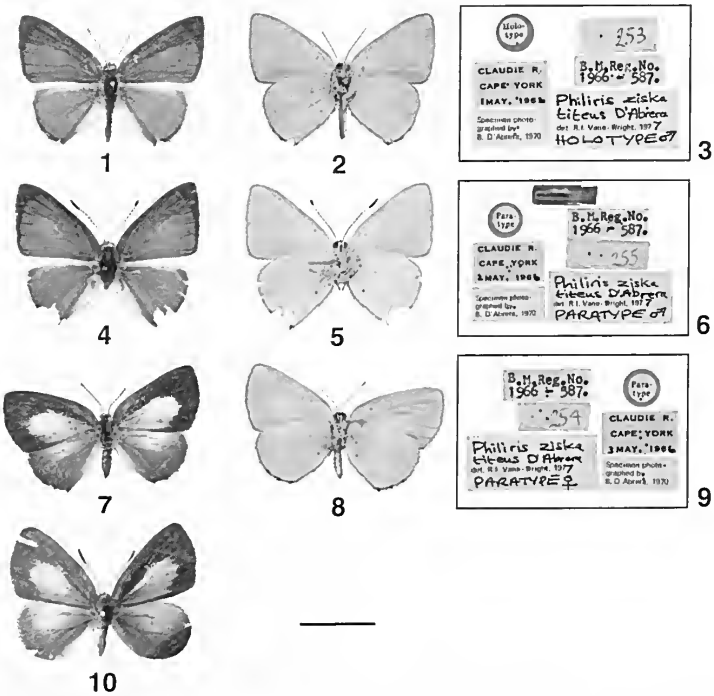
Kerr (1967) recorded *Philiris ziska* (Grose-Smith, 1898) from Australia based on a series of 11 males collected from near the Claudie River (now incorporated in Iron Range National Park, Cape York Peninsula, Queensland) during April and May 1966. Kerr's material was subsequently dispersed among three collections: Australian National Insect Collection, Canberra (ANIC: J. Macqueen and L.E. Couchman collections), Natural History Museum, London (BMNH), and his own private collection, Brisbane. Kerr (1967: 49) noted that two of his specimens were examined by lycaenid expert G.E. Tite, and commented on phenotypic differences in comparison with material from mainland New Guinea in the BMNH, but cautioned that "...the question of subspecific status must await further material". D'Abrera (1971), however, shortly proceeded to describe it as a subspecies *Philiris ziska titeus* D'Abrera, 1971 from Australia, based on material collected from Cape York Peninsula, Queensland, and illustrated three syntypes (2♂, 1♀) housed in the BMNH. Other than stating the range as "Claudie River (Cape York)" (D'Abrera 1971: 373) the label data of this material was not given, and D'Abrera neither provided a diagnosis nor indicated how the taxon differed from the nominate subspecies from mainland New Guinea. It has been assumed (Sands 1979) that the two males included as syntypes by D'Abrera (1971) in his description of *titeus* were, in fact, the same two specimens lodged in the BMNH by Kerr; however, because D'Abrera (1971) did not provide label data of the material examined this assumption has not been validated. Moreover, the location and to some extent the identity of the female have remained uncertain because this sex was not mentioned by Kerr.

Braby (2000) did not formally recognise *P. ziska titeus*, mainly because of the cautionary comments made by Kerr (1967), and Edwards *et al.* (2001) subsequently synonymised this taxon under the nominate species. However, Samson and Johnson (2009) recently reinstated the subspecies *P. ziska titeus* and noted several differences between the two subspecies. They also confirmed the identity of the female sex, which until that stage had not been determined with certainty. Compared with *P. ziska ziska* (Grose-Smith, 1898), adults of *P. ziska titeus* from Iron Range are smaller, the male frequently possesses a white suffusion in the postmedian area on the upperside of the fore wing (with the white are varying from few scattered scales to a prominent patch), and the female has more extensive white central areas on the upperside of both wings (Samson and Johnson 2009). Comparison of the illustrations of the two subspecies shown in D'Abrera (1971), Parsons (1998), Braby (2000) and Samson and Johnson (2009) indicate that *P. ziska titeus* male is also distinguished in having the black apex and termen of the fore wing broader, and the white costal streak on the hind wing more prominent and extending to the base.

In describing *Philiris ziska titeus* in his popular book, D'Abrera (1971) made reference to a 'type' specimen amongst the three he illustrated, but did not designate a holotype. That description is unquestionably valid, so the name is available from that work. Although the specimen was depicted above a large red spot, the spot is ambiguous because D'Abrera nowhere explicitly stated that specimens with red spots constituted holotypes, but made an implicit statement to the effect that "I have used type specimens in the illustrations...contained in the British Museum collections..." (D'Abrera 1971: 7). Furthermore, according to Article 72.1.2 of the ICZN (1999) regarding the use of the term 'type' relating to specimens, the name-bearing type is either a holotype if *fixed originally* or a lectotype if *fixed subsequently*. Hence, D'Abrera's vague reference to a type for *P. ziska titeus* does not constitute an original fixation, unlike, for example, *Pseudodipsas eone una* D'Abrera, 1971 in which he provided type data of the specimen with the red spot and used the word 'holotype' (D'Abrera 1971: 341).

Both Edwards *et al.* (2001) and Samson and Johnson (2009) referred to a 'holotype' of *P. ziska titeus*; however, this action is herein interpreted to constitute an incorrect subsequent fixation. Moreover, their nomenclatural action was based on an illustrated syntype and is not evidence that the specimen is fixed (Article 72.4.7). According to Article 73.2 of the ICZN (1999), all the specimens of the type series are automatically syntypes if neither the holotype nor a



Figs 1–10. *Philiris ziska titeus* D'Abrera, 1971 type material in The Natural History Museum, London (BMNH). **1–3**, lectotype male, showing upperside, underside and labels; **4–6**, paralectotype male, showing upperside, underside and labels; **7–9**, paralectotype female, showing upperside, underside and labels; **10**, paralectotype female showing upperside. Scale bar is 10 mm.

lectotype has been fixed. In other words, when a nominal species-group taxon has multiple syntypes, all have equal status in nomenclature as components of the name-bearing type. Further, Recommendation 73F states that where there is more than one specimen in which no holotype was fixed for a nominal species-group taxon established before 2000, an author should proceed as though syntypes may exist and, where appropriate, should designate a lectotype rather than assume a holotype. Examination of D'Abrera's syntypes in the BMNH indicate that R.I. Vane-Wright had earlier labelled one of the syntype males as 'holotype' and the two other specimens as 'paratypes'; however, these designations are incorrect because D'Abrera (1971) designated neither a holotype nor a paratype.

Therefore, in accordance with Article 72.2 (fixation of name-bearing types from the type series of nominal species-group taxa established before 2000) and Article 74.1 (designation of a lectotype) of the ICZN (1999) I hereby designate one of D'Abrera's syntypes as the lectotype to become the unique bearer of the name *Philiris ziska titeus* and to constitute a formal subsequent fixation since the name was first introduced almost four decades ago. This nomenclatural action does not affect the name of the taxon. Of the syntypes in the BMNH, the male specimen illustrated by D'Abrera (1971: 373) with the red spot below it is selected as the lectotype (Figs 1–3) because: (1) this is apparently the specimen that D'Abrera intended to be the unique bearer of the name *P. ziska titeus*; (2) R.I. Vane-Wright assumed that this was the 'holotype'; and (3) the specimen was previously illustrated showing the upperside, which portrays the diagnostic features of the taxon. The label data for the lectotype male is as follows: "CLAUDIE R., CAPE YORK, 1 MAY, 1966" [printed label prepared by J.F.R. Kerr], "Specimen photo-graphed by B. D'Abrera, 1970", "B.M. Reg. No. 1966-587.", "253", "Holo-type", "Philiris ziska titeus, D'Abrera, det. R.I. Vane-Wright, HOLOTYPE ♂". Comparison of the image of this specimen in D'Abrera (1971) with that of Figure 1 indicate damage to the antennae, with the clubs missing, but otherwise it is identical.

The two other syntypes illustrated by D'Abrera (1971) must now be regarded as paralectotypes, and not paratypes as considered by R.I. Vane-Wright or Samson and Johnson (2009). The label data for these paralectotypes is as follows: 1♂ (Figs 4–6) labelled "CLAUDIE R., CAPE YORK, 2 MAY, 1966" [printed label prepared by J.F.R. Kerr], "Specimen photo-graphed by B. D'Abrera, 1970", "B.M. Reg. No. 1966-587.", "255", "Para-type", "Philiris ziska titeus, D'Abrera, det. R.I. Vane-Wright, PARATYPE ♂". Abdomen stored in genitalia tube pinned beneath specimen; 1♀ (Figs 7–9) labelled "CLAUDIE R., CAPE YORK, 3 MAY, 1966" [printed label prepared by J.F.R. Kerr], "Specimen photo-graphed by B. D'Abrera, 1970", "B.M. Reg. No. 1966-587.", "254", "Para-type", "Philiris ziska

titeus, D'Abrera, det. R.I. Vane-Wright, PARATYPE ♀". Comparison of the image of the paralectotype female in D'Abrera (1971) with that of Figure 7 indicate damage to the antennae, with the clubs missing, and that the left fore wing has been dislodged and reglued, but otherwise it is identical. Comparison of the image and description of this specimen provided by D'Abrera (1971) with the diagnosis and illustration for the female sex of *P. ziska titeus* provided by Samson and Johnson (2009) confirm that the paralectotype female is conspecific with the lectotype male.

Examination by B. Huertas of other *P. ziska titeus* material housed in the BMNH revealed one additional syntype: 1♀ (Fig. 10) labelled "CLAUDIE R., CAPE YORK, 26 APR. 1966" [printed label prepared by J.F.R. Kerr], "B.M. Reg. No. 1966-587". This specimen must also be regarded as a paralectotype because it is part of the same series collected by Kerr and would have been available to D'Abrera. The only other specimen of *P. ziska titeus* in the BMNH collection is a male labelled "Potamon B.d., aww?, patria?", "EX MUSAEO, D^ris BOISDUVAL", "Ex Oberthür Coll., Brit. Mus. 1927-3.", the locality of which is indecipherable. This specimen has no claim to be part of the type series of *P. ziska titeus*.

It is curious that the two paralectotype females were part of the original series collected in 1966 from Iron Range by Kerr and sent to England, but no mention of it was made by Kerr (1967) or Sands (1979, 1980). Presumably they were misidentified by G.E. Tite and not recognised as being conspecific with the males of this taxon. Indeed, there was difficulty locating both female specimens in the main Lepidoptera collection of BMNH because they had been misidentified and incorporated with material of *Philiris nitens lucina* Waterhouse and Lyell, 1914 (B. Huertas pers. comm.), a taxon with which it closely resembles and with which it occurs sympatrically on Cape York Peninsula. Prior to confirmation of the identity of the *P. ziska titeus* female (Samson and Johnson 2009), Braby (2000: 683) remarked that "Females in Australia have not been determined with certainty, but specimens, provisionally referred to this species, have the blue areas along the dorsum below the white central patch on the upperside of the fore wing more extensive than in *P. nitens*. Further, the anterior edge of this area of blue is sharply defined, whereas in *P. nitens* females the blue suffusion merges with the white central patch." These two character states are evident in the paralectotype females and aid in distinguishing females of *P. ziska titeus* from those of *P. nitens lucina*.

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Crowley, L.M. 1949. Working class conditions in Australia, 1788–1851. Unpublished PhD thesis. University of Melbourne.

Sadlier, R.A. 1990. A new species of scincid lizard from western Arnhem Land, Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 7(2): 29–33.

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Volume 25, December 2009

CONTENTS

Short communications

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